BIOMOVE – CREATION OF A COMPLEX AND DYNAMIC MODEL FOR ASSESSING THE IMPACTS OF CLIMATE CHANGE ON CALIFORNIA VEGETATION

PIER FINAL PROJECT REPORT

Prepared For:
California Energy Commission
Public Interest Energy Research Program

Prepared By:
Conservation International

Prepared By:
Conservation International
Lee Hannah
Guy Midgley
Ian Davies
Frank Davis
Lydia Ries
Wilfried Thuiller
James Thorne
Changwan Seo
David Stoms
Nathan Snider
Commission Contract No. 500-04-2008
Commission Work Authorization No. MR-024, Amendment #1

Prepared For:
Public Interest Energy Research (PIER) Program
California Energy Commission

Beth Chambers
Contract Manager

Linda Spiegel
Program Area Lead
Environmental Area

Ken Koyama
Office Manager
Energy Systems Research Office

Martha Krebs
PIER Director

Thom Kelly
Deputy Director
Energy Research and Development Division

Melissa Jones
Executive Director

DISCLAIMER

Preface

The California Energy Commission's Public Interest Energy Research (PIER) Program supports public interest energy research and development that will help improve the quality of life in California by bringing environmentally safe, affordable, and reliable energy services and products to the marketplace.

The PIER Program conducts public interest research, development, and demonstration (RD&D) projects to benefit California.

The PIER Program strives to conduct the most promising public interest energy research by partnering with RD&D entities, including individuals, businesses, utilities, and public or private research institutions.

PIER funding efforts are focused on the following RD&D program areas:

- Buildings End-Use Energy Efficiency
- Energy Innovations Small Grants
- Energy-Related Environmental Research
- Energy Systems Integration
- Environmentally Preferred Advanced Generation
- Industrial/Agricultural/Water End-Use Energy Efficiency
- Renewable Energy Technologies
- Transportation

BioMove – Creation of a Complex and Dynamic Model for Assessing the Imparts of Climate Change on California Vegetation is the final report for the BioMove project (contract number 500-02-004), conducted by the University of California, Santa Barbara. The information from this project contributes to PIER's Energy-Related Environmental Research Program.

For more information about the PIER Program, please visit the Energy Commission's website at www.energy.ca.gov/pier or contact the Energy Commission at 916-654-5164.

Cite as:

Table of Contents

List of Figures

List of Tables

Abstract

There is substantial evidence that climate change is affecting ecosystems worldwide. California is no exception. With insights from historic climate change and subsequent species' responses, scientists are developing refined tools to evaluate how species change may continue in the future and what impact this may have on biodiversity and conservation. Accepted means of modeling the distribution of species have a number of shortcomings stemming from, among other things, their neglect of the ways individual species respond to changes in their habitats or the complex effects of competition between species. Furthermore, certain types of accepted models do not account for constraints on species dispersal, such as those imposed by disturbances such as land use change or fire. BioMove is a novel dynamic species modeling approach developed to address these issues. It simulates a target species in a dynamic landscape in competition with one or many different broader classes of vegetation. It integrates competition, dispersal, and disturbance models. It has important application potential for threatened species assessment, coordination of resource management efforts, modeling of invasive species into various localized biological systems, and other advanced climate change research.

Keywords: Climate change, emissions scenarios, species distribution modeling, dynamic species modeling, dispersal, disturbance

Executive Summary

Introduction

This project developed an advanced computer-based model, BioMove, that incorporates information about ecological niches, individual species populations and their dispersal, and ecological disturbance elements to simulate species range shifts in response to climate change. BioMove can simulate a variety of dynamic ecological processes, allowing researchers to explore problems in climate change biology that are difficult for other modeling tools to deal with but that are critical for estimating species extinction risk due to climate change and the biological implications of climate change policy.

The importance of species-based models is supported by past evidence, which indicates that species, rather than communities, are the unit of response to climate change. There is scant evidence for adaptation in place or large-scale extinction in response to most climate changes of the past 2 million years. Species movements that follow suitable climates are the most ubiquitous responses to past climate change. As species move to find a suitable climate for survival, communities are torn apart and reassembled. This response is expected in the future, making deciphering many questions of future climate change dependent on models that can simulate the fate of individual species.

Past climate change has driven species range movements over broad distances. Historically, migrations on regional to continental scales were common. In moist, cool upland areas, thousands of species moved through a region in times of rapid climate change. The various ways in which species disperse are therefore critical in determining whether species can reach and establish themselves in any newly opening suitable climate. In this sense, the future will be like the past — tracking of climate will depend largely on species' dispersal abilities.

However, the future also holds many differences for the fate of species movement as compared to the past. Land use changes that have now impacted most areas of the planet pose a major barrier to species' abilities to move to different areas — or shift ranges — a barrier that did not exist in the past. Human-induced climate change will be more rapid in most areas and of greater magnitude in many areas than natural climate changes of the past 2 million years. The frequency of events that greatly alter the landscape and replace entire plant and animal communities, such as fires and floods, has been greatly altered by human presence. The combination of these factors means that there is no precise way of predicting the future based on the past. Understanding future change requires combining several factors that are unique to human-induced climate change and modern land use.

An advanced modeling tool is therefore needed to simulate species range shifts in response to climate change. Essential elements of the model include shifts in suitable climate, dispersal, land use, and disturbance. Because no model fits all situations, ideally such a tool would allow interchange of different scenarios, for instance, substituting

different disturbance modules to allow fire simulation in systems in which fire heavily influences species' dispersal, or substituting different grazing models where livestock pressure is the greater disturbance. Since dispersal over long distances involves multiple generations, simulation must include life history parameters of individual species such as fecundity and time to reproduction.

Purpose

This project developed a tool for dynamic modeling of species' distributions under climate change. This model is suitable for biogeographic and landscape studies, advanced climate change research, and ecosystem management planning. The project also intended to test the feasibility of combining several modeling approaches into a single combined modeling tool.

Project Objective

The project objectives were to

- Develop a hybrid, dynamic modeling approach (BioMove) to represent the ways plant species respond to climate change.
- Test the model to illustrate potential applications for BioMove.

Project Outcomes

Results from this project provide a new tool available for public use to predict species movement under climate change. This hybrid model, BioMove, incorporates niche, population, dispersal, and disturbance elements into an integrated whole. As a model that can simulate many ecological processes across time and space, BioMove allows exploration of problems in climate change biology that have been difficult for other modeling tools. BioMove can simulate dynamics critical to estimating species extinction risk due to climate change, biological implications of climate change policy, and other problems with biodiversity associated with environmental change.

BioMove is carried out in an existing package of landscape modeling software (LAMOS) and can incorporate differing dispersal and disturbance modules. BioMove uses climate suitability as a starting point and then examines how dispersal, population establishment, growth, and reproduction can lead to population spread into newly suitable climates. Competition is simulated using trait-based plant classifications known as plant functional types (pft) —pft are determined, for example, by how plants acquire light and nutrients or how they interact with a given disturbance, such as fire or grazing. The population elements of BioMove allow simulation of advancing or trailing edge population dynamics.

Examples presented in this report include modeling of sugar pine, blue oak, Joshua tree, and invasive grasses. The development and archiving of species distribution models for a wide variety of unique California species for use in BioMove is described.

Conclusion

As a result of this project, a new tool — BioMove — is available for public use to dynamically model species distribution. It provides unique attributes that allow users to create parameters for a simulation for specific species and plant functional types. Climate change impacts are driven by complex interacting factors, something BioMove is uniquely positioned to address among species-based models. This novel approach to modeling species distribution under climate change has many applications for California and beyond.

Recommendations

Natural resource managers, private land holders, and policy makers can consider BioMove as a tool for informed decision-making when assessing likely impacts from climate change. Applications of BioMove include assessing the extinction risk of species due to climate change, selecting protected areas that are viable now and in the future, managing timber and fire in public lands, assessing threats posed by invasive species favored by climate change, measuring changes in ecosystem services due to climate change, quantifying changes in vegetation due to air pollution, and examining the biological implications of different policy options for combating climate change. Case studies of climate change impacts indicate that the model is useful for addressing the different ways fire affects species and ecosystems, patterns of human-related land use, and varied topography — all critical elements of the dynamics of climate change and nature in California.

Benefits to California

Among the potential applications of the model are the exploration of fire-vegetation interactions under climate change, modeling localized events, investigation of scenarios in which greenhouse gases stabilize and the effects of those scenarios on biodiversity, examination of the effect of land use management options on species composition as climate changes (for instance, in timber lands), and integrating BioMove with models of ecosystem services.

One of the most striking features in California landscapes is the importance of fire in determining the long-term fate of species range shifts and vegetation structure. For instance, oak species at lower elevations in the Sierra Nevada have expanding suitable climate at higher elevations as climate warms but may have difficulty occupying these newly suitable areas since they are already occupied by mixed conifer forest in which the lowland oaks have difficulty recruiting. When fire enters this system, the conifer forests are removed, allowing upslope migration of the oaks. Without fire, mature oaks are slowly squeezed out of their current range. Fire management is therefore critical in managing climate change impacts on California species. Fire management is, of course, a complex and politically charged issue in its own right. It is made more complex by climate change but potentially more easily managed because of the availability of an advanced modeling tool such as BioMove.

All of these are timely issues in California that will benefit from advanced modeling tools. Questions of changes in biodiversity across space and time and involving changes in landscape are an especially fertile ground for BioMove enquiry. Broad availability of BioMove to the research community will stimulate many additional applications.

1.0 Introduction

1.1. Background

Climate change is affecting ecosystems worldwide (Parmesan and Yohe, 2003; Root et al. 2003). Species ranges are shifting, corals are bleaching and the timing of biological events is advancing as the world warms (Walther et al. 2002). These impacts have important consequences for conservation (Hannah et al. 2002). Extinction risk from climate change has been projected to affect from under one tenth to as much as half of all species in biodiversity hotspots such as California (Malcolm et al. 2005). To anticipate and respond to these looming impacts, scientists are constructing models of possible biotic response to climate change. Models of coral bleaching (Hoegh-Guldberg et al. 2007), change in vegetation structure (Cramer et al. 2001), change in timing of events and shifts in species ranges (Peterson et al. 2002) are all important tools in understanding and responding to the threat that climate change poses to nature.

To predict how the biological consequences of climate change may unfold in the future, it is helpful to examine records of historic climate change and associated ecosystem responses (Overpeck et al. 2003). These insights from the past allow scientists to construct models of possible future ecosystem and species responses to climate change.

As the climate oscillated between glacial and interglacial periods throughout the Pleistocene, species distribution and community composition also changed (Graham and Grimm 1990, Huntley and Webb 1998). In some cases, levels of diversity remained consistent. For example, a biodiversity hotspot in the Peruvian Andes maintained high levels of biodiversity through a 6-degree warming transition into the Holocene (Bush et al. 2004). Vegetation responded to changes in climate by migrating with latitude or elevation, avoiding extinction (e.g. Flenley 1998).

Past biotic response to climate change was clearly dominated by species range migrations, and these range changes were unique to each species (Huntley 1991). Species tracked suitable climatic conditions during past climate change, with ranges tracking climate latitudinally but also up and down slope in warming and cooling episodes. These range changes covered hundreds of kilometers and entire continents in some cases (Coope 1995).

A major difference between past and present climate change is that many of the historic shifts that took place were on a much longer time scale of climate change than the athropogenically induced climate change we are experiencing now (Overpeck et al. 2003, Bush et al. 2004). Present day increased greenhouse gas emissions are associated with increased global mean annual temperatures which are expected to keep rising throughout the next several *decades* (Houghton et al. 2001). Under our current trajectory of greenhouse gas emissions, general circulation models predict continued warming and drying throughout much of California (Hayhoe et al. 2004).

In addition to gradual historic climate change, there were rapid events, more analogous to the present day changing climate. Historic pollen records suggest that rapid migrations in vegeta0tion did occur in response to these short term changes in climate (Gear and Huntley 1991) allowing species persistence

Following these same principles of tracking species movement in response to past climate change, scientist have developed methods to predict where species will be found in the future. One such approach to examining individual species' response to climate change is bioclimatic envelope modeling, or niche-based modeling. The primary strength of bioclimatic envelope modeling is its reliance on the concept of the ecological niche (Grinnell 1917; Hutchinson 1959) and the abundance of data that can be used to derive the niche. Given a scenario of future climate conditions, it is possible to predict the new geographic realization of the niche. Prior studies have used bioclimatic envelope models to predict individual species distributions under modeled future climates (e.g. Heikkinen et al. 2006; Pearson and Dawson 2003; Thuiller 2003). The compilation of many individual species distribution models for a common region can serve as arguments for habitat conservation or be used in hybrid models. One such study predicts >40% species extinction in Mexico, including birds, mammals and butterflies (Peterson 2002).

Recent review papers suggest that current approaches in predicting species' response to climate change are inadequate and highlight a need for a more comprehensive approach (e.g. Botkin et al. 2007, Thuiller et al. 2008). Indeed, there are several shortcomings of species distribution models. Firstly, they do not realistically account for population-level processes especially at the leading and trailing edges of geographic ranges. They do not consider such population phenomena such as persistence in sub-optimal climate conditions and dispersal and establishment of populations in new geographic ranges that may affect extinction risk (Harte et al. 2004). Secondly, they do not account for community interactions and processes such as inter- or intra-specific competition (Davis et al. 1998) or disturbances such as fire (Davis 1994).

It is evident that species distribution models fail to address the dynamic nature of populations and do not account for dispersal constraints, changes in disturbance regimes or species interactions. Regardless of the niche described by climatic and/or soil limitations, a species will not realize a potential niche if limited by certain life history constraints. Life history traits and mean dispersal rates seemingly should aptly describe the rate at which a species could migrate across the landscape. However, evidence from the pollen record challenges this explanation of species movement, known as "Reid's Paradox" (Clark et al. 1998). It states that evidence from the pollen record suggests that migration happened much faster than predicted from simple radiation dispersal models. There must be another mechanism that allows species to colonize new habitats.

One such mechanism could be long distance dispersal events (e.g. carried by a river, stuck to a mammal, human assisted transport). However, the importance of long distance dispersal to species tracking environmental change may vary depending on

landscape fragmentation (Pearson and Dawson 2005). Advances in modeling long distance dispersal help to elucidate how these events may effect species migration (Pearson and Dawson 2005, Clark 1998). These advances must be incorporated with species distribution models to more comprehensively project if and where species may migrate in the future.

More advanced methods of simulating how species distribution will shift under climate change are needed for multiple reasons. California is an especially fertile testbed for application of such methods. California hosts a heterogeneous array of vegetations types including many species endemic to the California Floristic Province. How vegetation in California will respond to climate change is of paramount interest to foresters, land managers, conservation groups, developers and individual land owners. It will also affect the persistence of dependent species thus affecting overall ecosystem health and stability. In California, climate change is likely to result in the poleward and upslope movement of species, effects already seen in other parts of the earth (Parmesan et al. 1999). These effects may be confounded by land use change as California's population continues to grow and place greater demands on its natural resources. In order to maintain the biological integrity of California's ecosystems and the services they provide, we must develop better predictive tools for assessing species' response to climate change.

1.2. Project Objectives

To address the shortcomings of current predictive modeling approaches for species under climate change this project has developed a modeling approach that utilizes species distribution models as input but includes sub-models to account for other factors that may affect if and where a species can migrate. The purpose of this study was two-fold:

- Develop a hybrid, dynamic modeling approach (BioMove) to model plant niche realization under climate change.
- Parameterize the model to illustrate potential applications for BioMove.

1.3. Report Organization

The remainder of the report consists of three sections. Section 2 provides a description of the BioMove model, the component models and its user operation. Section 3 outlines potential applications of BioMove. Section 4 contains five examples of BioMove simulations. Five ecoregions consisting of different target species-plant functional type combinations throughout the state are described in detail. Specific attributes of the model were implemented in each simulation to highlight the unique qualities of BioMove. The description of each case study includes the parameterization inputs and model results to provide readers with a more comprehensive experience of BioMove. In Section 5, the authors provide a synthesis of recommendations for future research. The appendices contain additional screenshots of model simulations, species distribution

modeling methods used to generate input data and parallel type examples for mammal species.

2.0   BioMove Model Description

This section provides an overview of the BioMove model. It discusses the underlying theory considered in the design of the model, describes the processes simulated within BioMove, and outlines the model flow and user interface. It briefly describes the parameter and operating system requirements as a guide to users considering implementation of the model.

2.1.   Model Overview

BioMove is an integrated niche and population modeling approach for assessing species range dynamics and persistence under climate change. The model is implemented within the Landscape Modeling Shell (Lamos) software, which allows ready interchange of other model elements, including disturbance modules and dispersal modules. Competition is represented between a target species and user-defined plant functional type, both of which respond to disturbance and changing climatic suitability. BioMove allows investigation of species' ability to occupy newly available niche space as climate changes, in a simulated landscape in which relevant factors such as disturbance, competition, and dispersal are represented.

The central idea behind BioMove is to simulate a species' ability to realize newly available suitable climatic space as climate changes. Since that new niche space may be separated from existing niche space by non-natural land uses and be affected by the species' dispersal ability, these factors have been built into the BioMove/Lamos framework. Dispersal is often constrained by disturbance events in the landscape, particularly fire. Consequently, fire simulation capability is built into BioMove. A grazing simulator is available as well, and other disturbance events may be defined by the user. When climatic suitability moves across large distances, as is expected in human-induced climate change this century, multiple generations of a species may be involved. Individual propagules may need to disperse to a newly suitable location, grow, reproduce and disperse again to keep pace with rapidly moving suitable climate. BioMove includes a population model to simulate these processes.

BioMove is a flexible tool thanks to its implementation platform, Lamos. Multiple disturbance and dispersal regimes can be represented, either in parallel or as alternatives to one another. For instance, three fire simulators are available in Lamos. In testing of BioMove, and in the descriptions below, we have used a base configuration which consists of a contagion fire simulator and a kernel dispersal function. The capabilities of BioMove will be described under this base configuration. Where other configurations are possible, the base and alternative configurations will be mentioned.

BioMove has been designed and tested to work with plant species. This is because plant species disperse relatively poorly relative to most vertebrate species, making simulation of their dispersal dynamics more complex and challenging. BioMove might be adapted for vertebrate application with relatively minor modifications, but many aspects of the

model needed to usefully simulate plant dispersal would not be engaged in a vertebrate simulation.

BioMove models an individual *target* species within an interacting landscape. The target species reacts to climate change through its climatic niche. As the climate changes, the target species' niche migrates to track suitable conditions and the range within BioMove is updated. There are several options for loading a climatic niche into BioMove, the base configuration uses a niche model or PCA analysis. Niche models such as GAM, GARP or Maxent may also be used. BioMove has been tested using both the PCA and statistical niche (or *envelope*) models.

The BioMove target species is affected by climate and landscape interactions and dynamics, including competitor plant life forms and disturbances. Competition can affect a species ability to grow, reproduce and track suitable climate. To account for this effect, a competition model, FATE has been adapted to operate within BioMove. The competition routine uses generic plant types which compete with the target species. The competitors affect the target species through user-provided parameters. For instance, an understory species can be parameterized to do poorly in open, low competition but high light settings.

The model uses a niche model (see introduction) or a PCA of present and future climate variables to derive the habitat suitability for the target species in any given pixel. The basis of the PCA approach is that the distance to the origin of the PCA for multiple climate variables equates to the distance to the centroid of the niche in multi-dimensional niche space. The geographic fit obtained with the PCA approach is "looser" (more commission) than most statistical niche models (eg, GAM, GLM), but it provides a better approximation of fundamental niche. One way to conceptualize the use of PCA in BioMove is that the PCA provides the fundamental niche, while the other components of BioMove help to resolve the realized niche.

The model is implemented annually. In the base configuration, climate change is implemented in decadal timesteps driven by user-provided surfaces. However, the climate timestep is user defined, and any interval of climate change may be defined using the scheduler. Decadal steps have been used in testing because annual climate change requires longer runs and more input preparation without substantially altering most results. Decadal climate change increments are recommended unless unusual very rapid change is indicated.

The grain of the simulation is defined by the user, and is often determined by the resolution of available climatologies. Testing has been conducted at a 1km (30 arc second, approximately 0.86 km) grain, which is the finest grain at which downscaled global climatologies are available. 1km is appropriate for landscape-to-biogeographic scale analyses for many species. Coarser grain may be more practical for regional or continental studies of more widespread species, because run time scales with the number of grid cells in the domain. Finer grains can be implemented in BioMove for

site-scale analyses, but climatologies at finer scales would have to be constructed from non-traditional (i.e., non-GCM) sources such as microclimate models.

BioMove simulates the vegetation structure of the selected area defined by plant functional types (PFTs) using the FATE succession model (Fig. 1) (Moore & Noble 1990). In the field of ecology, the definition of PFTs varies by author and context but broadly can be considered as those species that require similar resources and fulfill the same set of functions in an ecosystem. They may share common responses to disturbances, exhibit similar phenological patterns and/or patterns of leaf senescence. The term is used in vegetation modeling to be roughly synonymous with vegetation type. For instance, 'mixed conifer forest' and 'deciduous broadleaf forest' are examples of PFT from vegetation models.

BioMove uses PFTs to denote one or more species, usually a group, that have similar roles with respect to competition and disturbance in an ecosystem. For example, a group of shrubs that re-sprout after fire would form a PFT distinct from shrubs that are only established by seed after a fire. Growth form is another important PFT distinction in BioMove, as it plays an important role in resource competition. A scrub oak and a tree oak would therefore fall into distinct separate PFTs even if they were closely related taxonomically.

The PFTs used in this model are chosen based on their relevance to the ecosystem studied, and are therefore finer than those used in dynamic vegetation models (DVM, Smith et al. 2001).For instance, a usual plant functional type used by DVM is C3 grass. Although highly relevant for ecosystem functioning, it lacks the response to disturbance for instance, where C3 grasses can be either a seeder or re-sprouter. In highly disturbed habitats like alpine ecosystems (fire, grazing), a plant functional type must include such a discrimination. For instance, in the fire prone Cape Floristic Region, a practice simulation created five different plant functional types based on fire response, shade tolerance/intolerance, and structure. One plant functional type was evergreen trees, not adapted to fire, non- re-sprouter, shade-tolerant at germinant and immature stages. Another plant functional type was "Protea", tall shrubs, fire-adapted species, re-sprouter, shade intolerant at germinant and immature stage. Such plant functional types, relevant to particular ecosystems are relatively easy to develop with the basic knowledge of field biologists.

BioMove needs basic parameters to simulate the PFT, including their competitive ability at different life stages, their dispersal ability (dispersal model), their mortality and regeneration responses to fire, grazing and other disturbances relevant to the study area (disturbance model). This information is taken from literature, trait databases, field measures and detailed knowledge of the researchers. Until now, only competition for light is simulated using recent developments from the FATE model (Moore & Noble 1990), but competition for soil resources will be a substantial addition in the next developments. For seed dispersal, the dispersal module of Lamos enables alternative

assumptions about the dispersal ability of each PFT (Higgins *et al.* 2003b) such as the presence or not of stochastic long-distance dispersal events.

Soil characteristics could also be parameterized from existing maps and used to limit seed dispersal and growth rate. In a similar way to any landscape model, the succession model simulates the dynamics of plant functional types assuming that the environment is optimal. The novelty here is to simulate the potential habitat suitability of the plant functional types with a niche-based approach using environmental variables (e.g. climate, topography, soil) under present conditions. This habitat suitability allows the abundance of the plant functional types to be constrained using different functions (linear, Gaussian, logarithmic). A habitat suitability of one is assumed to be an optimal habitat, while a HS of 0 for instance, prevents the establishment of the given plant functional type. The niche model allows the production of the habitat suitability for each modelled plant functional type every year based on different climate and/or land use change scenarios, see after) (Fig. 2. Flow diagram). Finally, BioMove runs using four or more age-classes and track cohorts at every time-step (in this case annual time-step).

2.2.   Processes Simulated Within BioMove

Four types of processes are simulated in BioMove. Classes of model processes in a typical implementation include: ecosystem, population, community and landscape.

1) Ecosystem processes: The interaction of physical and biological processes. They only address life history issues where they differently parameterise processes relevant to light and water functions. The key ecosystem process simulated in BioMove is the influence of climate (present and future) on the distributions of species and plant functional types.

2) Population process: A single-species demographic model counting discreet quantities of individuals. By implementing a population model in landscape format it becomes a meta-population model exchanging individuals through migration or dispersal between sites. Population processes — birth and death rates for a single species — parameters describing interactions are not required. For a meta-population model, landscape type parameters must be introduced.

3) Community process: The interplay of life history (genetics) attributes between species or plant functional types. (Reproductive strategies, disturbance response, shade tolerance and height).

4) Landscape process: Any process that is modeled through the spatial propagation or correlation of events/material/energy through time. These include seed dispersal and fire. This is not to say that these processes must be dealt with as landscape processes but are good candidates. Landscape processes have both qualitative and quantitative parameters addressing distance and rates.

Climate change is the primary ecosystem process BioMove is intended to simulate. It does this by driving geographic change in the distribution of the target species through a niche simulation. As climate changes, the niche changes, resulting in change in habitat

suitability across the range of the species, as well as shifts in the areas inside and outside of the niche (suitable climate space). As described above, climate change occurs in 10 year timesteps, each timestep interpolated between 30-year normal climatologies obtained from a global climate model (GCM).

Population processes are modeled using a stage and age-based population simulator. The model initiates by populating suitable cells with an initial population comprising four life stages, and spins up for several hundred years to achieve a stable meta-population. A mixed age/stage population demographic model is implemented in each cell, with age to first reproduction defined, but a stage-based matrix implemented post-reproductive age. Reproduction is parameterized per life stage, but spatially stochastic reproductive processes such as mast fruiting are implemented using a spatially discrete approach that simulates measured or inferred spatial and temporal variation.

Community processes, especially competition, are modeled using a plant functional type approach. BioMove generates a dynamic community of competing plant life forms (functional types) at the landscape level, which also perform according to climate suitability. This landscape of competing functional types is able to suppress the target species (depending on parameterization through shading or other forms of resource depletion), but the target species does not affect the functional types (asymmetric competition). The functional types also serve to develop the biomass necessary to drive other landscape level processes, such as to fuel fire disturbances. Competition is expressed through functional types rather than individual species to reduce the number of parameters needed to define the competitive interactions. Because competition is exerted from the plant functional types to the target species, but not the reverse, the practical impact of consolidating many species into a few functional types is minimal.

Landscape processes simulated in BioMove include dispersal and disturbance, particularly fire. Lamos provides the opportunity to implement multiple dispersal and disturbance modules. In the base configuration, dispersal is modelled using a kernel approach, with seeds dispersed annually or on an environmental cue such as fire (for serotinous species), though other dispersal modules may be substituted by the user. Disturbances are user defined, and can include fire, grazing, windfall or management impacts. A contagion fire model is implemented in the base configuration, but other fire models are available. A dynamic grazing disturbance module, 'patchgraze' is available. An unlimited number of additional disturbances can be programmed by the user as masks, each with user-defined impacts on the target species and plant functional types, using the scheduler.

2.3. Model Flow

BioMove has two major functional components, one for the target species and one for the plant functional type. Within each, dispersal, disturbance and demographics are simulated, as well as the effect of climate change, as illustrated in Figure 2.3.1, below. The two functional components interact through the competition term, in the figure

illustrated as competition for light. The plant functional types exert influence on the target species through this interaction. It is a unidirectional interaction, in that the target species does not exert competitive pressure on the plant functional types, as indicated by the one-way arrow in the figure. The target species and plant functional type interact in other ways mediated by disturbance and the landscape. For instance, the presence of a plant functional type can increase fire frequency and decrease target abundance due to frequent burning. These indirect interactions are difficult to capture in a simple schematic and are therefore omitted from Figure 2.3.1.
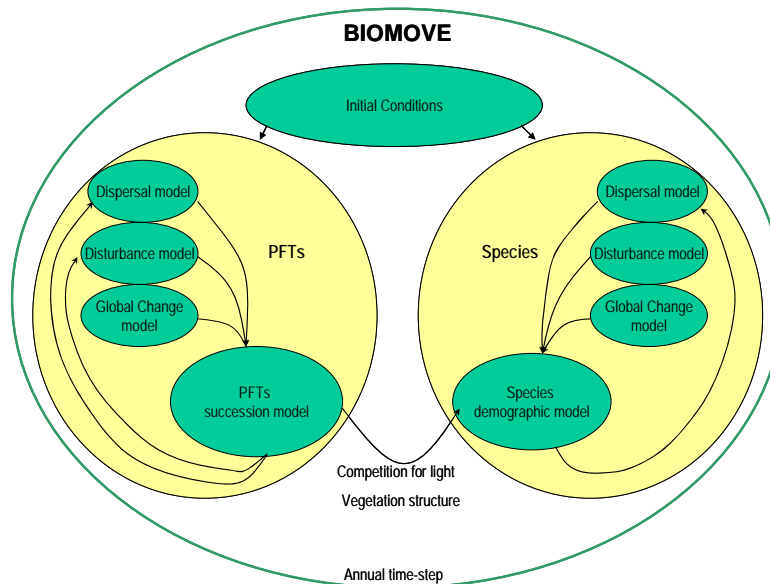
Figure 2.3.1. Schematic flow diagram of BioMove model.

The model proceeds from initial conditions (see the top of Figure 2.3.1) which inform abundance and location of the target species and plant functional types being used, among other factors. These initial conditions are usually generated by spinning up the model for several hundred years based on neutral or estimated values. The initial conditions are then saved to a file which can be used in model initiation for runs involving that target species and plant functional type combination.

Climate change is simulated in the Global Change sub-module of both the plant functional type and target species. It is generated internally from external climate files when the PCA approach is used, thus it is shown as an internally-sourced element in Figure 2.3.1. However, it can also be simulated using range maps of target species distribution at different timesteps, generated by niche models such as GAM or by expert opinion, in which case it is generated offline and supplied external to the model.

Within the two major functional components, the demography of the target species is the most complex sub-component, as illustrated in Figure 2.3.2. Plant functional type demography is a simplified version of the same scheme. The growth and reproduction

14

of individuals is simulated in three life-stages, each comprised of multiple timesteps. For example, it can be defined that there is a juvile, non-reproductive lifestage that lasts five years, or five timesteps, a subadult life stage that lasts 20 years, and then an adult, fully reproductive life stage that lasts 100 years, in the case of a tree.
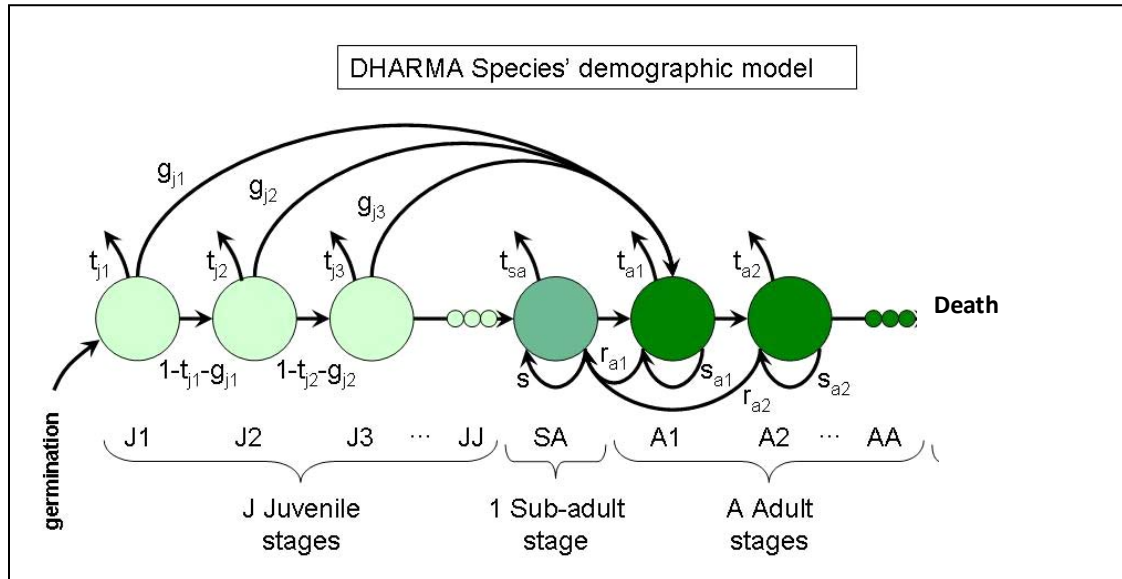
Figure 2.3.2. Schematic flow of BioMove demographic model (target species).

Reproduction is parameterized per life stage, but spatially stochastic reproductive processes such as mast fruiting are implemented using a spatially discrete approach that simulates measured or inferred spatial and temporal variation. It differs from animal population viability analysis (PVA) in only having undirected movement between patches (kernel seed dispersal).

Different biological traits are necessary to parameterize this demographic model, like life-span, whether the species is a re-sprouter or a seeder, if the species needs a disturbance to release propagules (fire or grazing/mowing). Similarly, the dispersal ability of the species is also required (mean dispersal distance, fraction of seeds long distance dispersed).

A unique feature of BioMove is the fact that the plant functional type-succession model defines the vegetation structure of each modeled pixel and thus the light availability (or other resource competition) at different inferred height strata (or other resource competition mediating functions inferred from vegetation age or population density). This simulated light or other resource availability is then used inside the species demographic model to simulate the competition for resources between the vegetation and the modeled species, depending on user defined resource effects (such as shade tolerance or intolerance at different life stages).

BioMove runs for as many years as the operator defines, with vegetation age and composition updating at each step from the demographic model and influences such as disturbance. Changes in a plant functional type in one timestep affect target species growth and reproduction and disturbance intensity and other factors in the subsequent step. The length of run depends on the properties of interest. Runs of multiple centuries will be required to assess the ultimate conservation fate of species, while runs of decades may be sufficient to assess transient behavior in this century. For instance, BioMove can run for many centuries to a new presumed equilibrium climate, or it can be run for 50-100 years to simulate only the upcoming period of rapid transition this century.

2.4. User Interface

The BioMove user interface is a fully operational GUI, with dialog boxes and parameter entry capability for all values necessary for model operation. The overall interface is implemented with Lamos, the Landscape Modeling Shell software. Access to dispersal and disturbance modules is through Lamos. The BioMove base configuration is the combination of the BioMove succession/population module with the kernel dispersal and contagion fire modules. To edit modules composing the model, for instance to substitute a different fire model, the operator uses the edit model configuration interface in Lamos. Within Lamos, there are parameter entry tabs for life history, resource response, morphology and BioMove (or "Dharma" in beta versions). The life history, resource response and morphology tabs all refer to the plant functional type. The BioMove tab is used to parameterize the target species. Within the target species space, there are entry tabs for demography, competition, disturbance, envelopes and dispersal. These entry pages will be described with reference to accompanying screen shots on the pages that follow. The BioMove users manual is intended to provide detailed guidance on parameter entry for the model, so this overview is provided as a complement to that resource, to give those not yet familiar with the model an overview of its parameter requirements and capabilities.
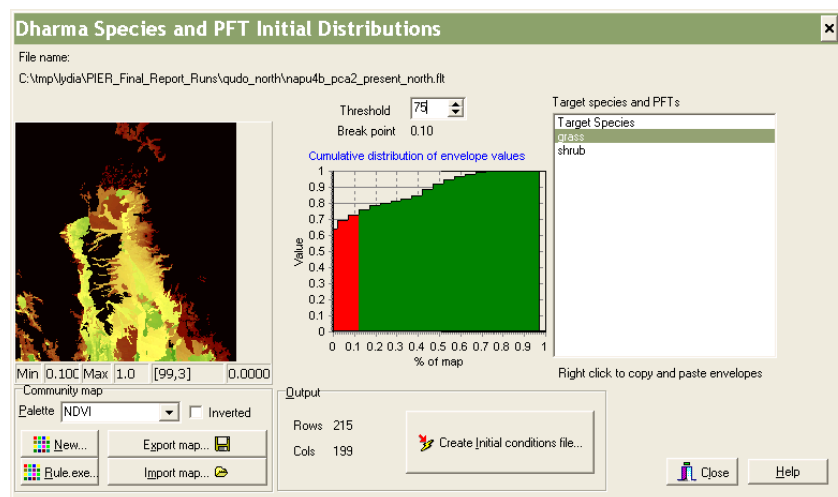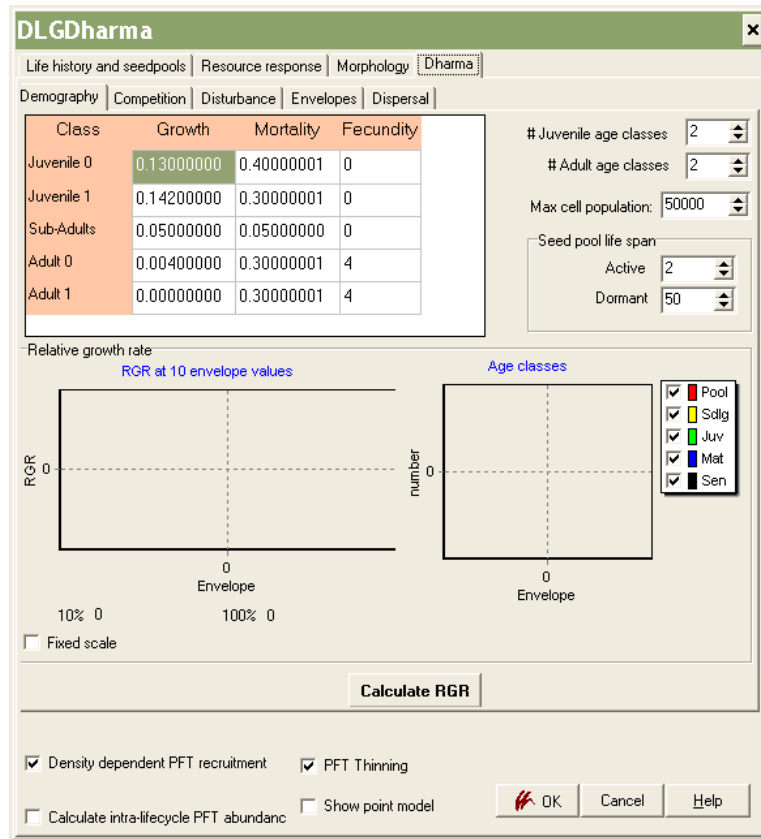
Figure 2.4.1. The initial conditions menu.

16

The initial conditions file provides the baseline from which the model simulation begins to run. The file is built from the "Initial Conditions" menu by adding a map for the target species and each of the plant functional types. A threshold is set discriminate low envelope values which will affect the time to which a species reaches equilibrium. Once an initial conditions file is created, it can be used to spin-up the system to equilibrium. This is then saved and used as the initial conditions file for subsequent simulations.

Figure 2.4.2. Target species demography dialog menu

The target species demography dialog allows user entry of species growth, mortality and fecundity for several life stages. The number of classes within each life stage is first defined (upper right of dialog box), then the appropriate growth, mortality and fecundity values are entered for each of the life stages (upper left of dialog box). The total population allowed in each grid cell is set in the dialog just below the dialogs for setting the number of classes in each life stage. The relative growth rate (RGR) resulting from the parameters given for each life stage may be calculated in the lower portion of the tab by clicking on the "Calculate RGR" button. If the relative growth rates do not agree with values expected, growth and mortality values must be readjusted.

17
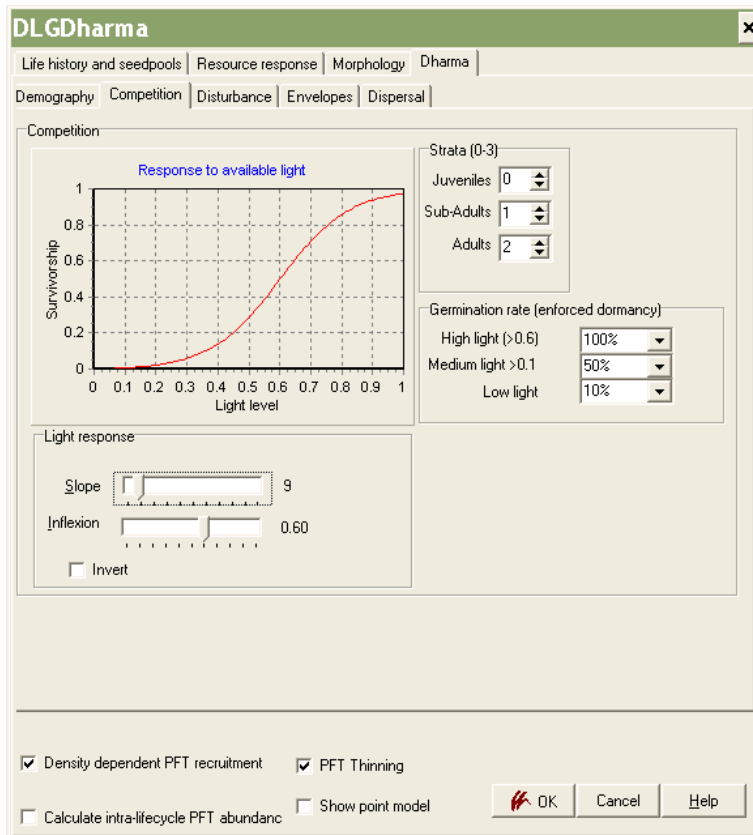
Figure 2.4.3. Target species competition tab.

The target species competition tab allows definition of the relative response of the target species to the resource mediating competition. The dialog boxes are denominated for light competition, but other resource competitions, such as competition for water in arid environments in which light is not limiting may be conceptually treated by the model. Adjustments are provided that allow the response curve to the competition resource to be shaped (slope, inflexion, invert).
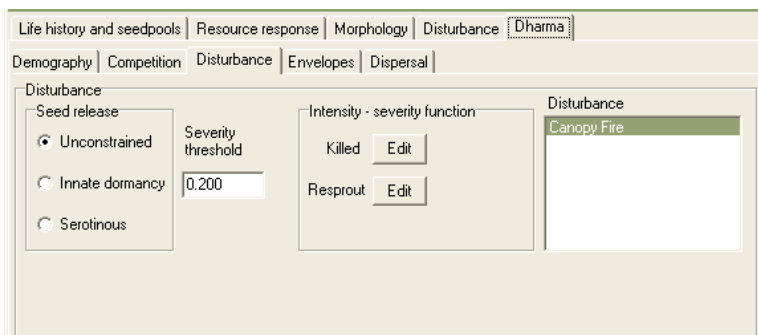
Figure 2.4.4. Target species disturbance response tab.

Disturbance response constrains target species behaviour when a disturbance occurs. Disturbances are loaded in the model configuration window (not shown) and appear in

the right hand side window (e.g., "canopy fire" in figure above). Any number of disturbances may be loaded, so an actual run might list "canopy fire", "ground fire", "grazing" and other disturbances. This tab allows each disturbance to exert a different response in the target species. For instance ground fire can be configured to kill all juveniles of a tree species, while mature trees are spared. For the same species, canopy fire response can be high mortality in all life stages, including mature trees. Disturbances can be dynamically simulated in the case of fire and grazing, or loaded as masks in the case of other disturbances. Dynamics in other disturbances can be simulated offline and added as annual masks, with the scheduler calling a new mask at each timestep. In the case of fire, relevant life history characteristics are requested. The user may define whether the target species reseeds or resprouts after fire, and whether such behaviour is obligate. Serotiny, the characteristic of holding seeds in cones over multiple years that are only released by fire, can be defined in the appropriate checkbox. In total, the disturbance interface provides users with a complex set of disturbance responses that can be simulated for any number of disturbance types, all of which may operate simultaneously.
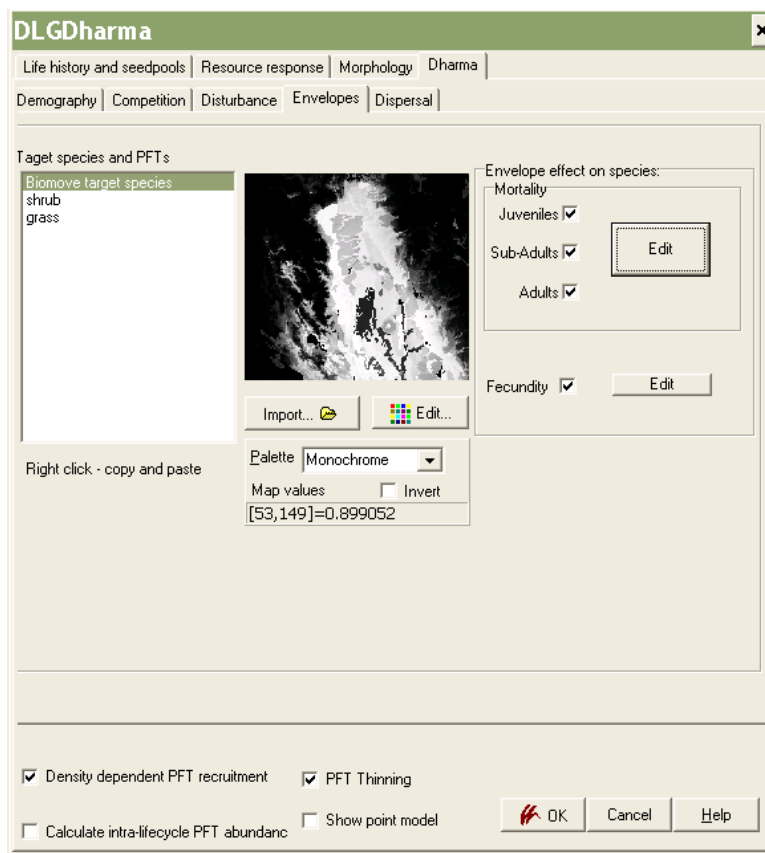
Figure 2.4.5. Target species habitat suitability tab

Target species habitat suitability and therefore response to climate change, is defined in the 'envelopes' dialog. The "envelope" is generally the envelope of suitable climatic

conditions for the species, roughly analogous to the species' niche. Habitat suitability is calculated internally in the PCA routine or externally with species distribution models such as GAM or MaxEntropy. Loading species distribution models based on future climatologies from global climate models allows climate change to be simulated. Climate change can be simulated at timesteps as fine as annual by interpolating climatologies from GCMs. BioMove has been tested using climate change at decadal timesteps. This captures time dynamics more robustly than using only 2050 and 2080 scenarios, yet is much less data-preparation intensive than annual change. The envelope dialog tab allows setting differential effects of climate change on different life stages. For example, juveniles may be more sensitive to climate change and can be set to suffer greater mortality, for instance in drier scenarios.
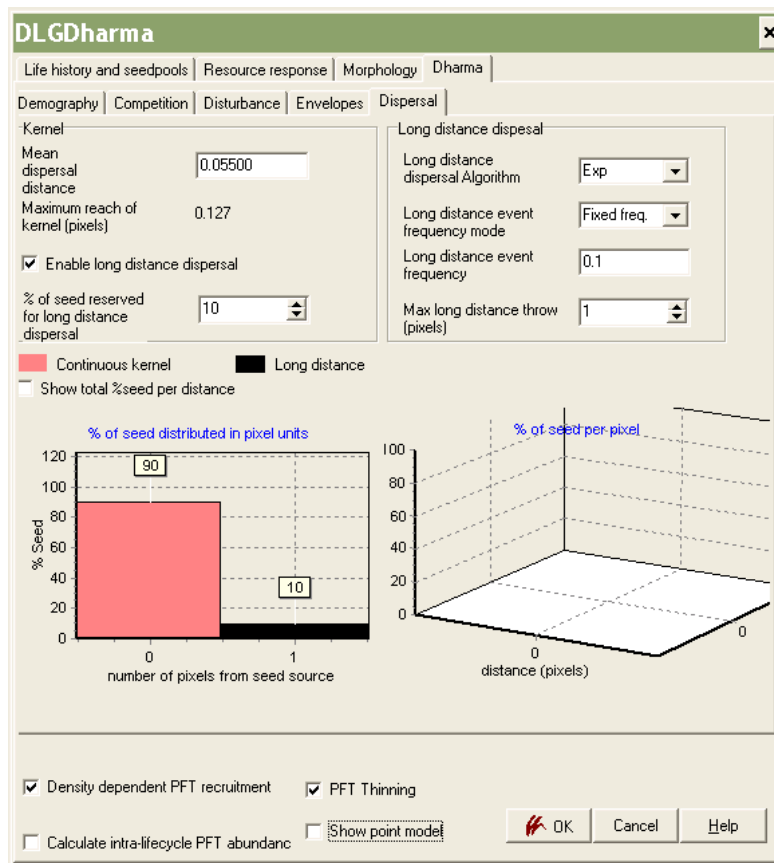
Figure 2.4.6. Target Species dispersal tab.

Target species dispersal is simulated as a dispersal kernel — a distribution of propagules away from a grid cell. Every grid cell in the simulation that has target species population will produce "seed" or propagules. How far those propagules can establish from the parent cell is determined by the dispersal function. Recent dispersal research and theory suggests that "long tails" in this dispersal function, that is, rare long distance events, play an especially important role in species' tracking of rapid climate change across long distances. This long-distance dispersal probability is simulated especially well by this

dispersal kernel approach. The user defines the mean dispersal distance and maximum distance of dispersal as well as the proportion of seed in each distance category. The interface returns both a bar graph (left in illustration) and 3-D representation (on the right) of the decline in dispersal with distance. For species with unusually heavy seeds or unique dispersal syndromes, long distance dispersal can be turned off.

2.4.1. *Plant Functional Type Inputs*

BioMove has input dialogs for plant functional type life history, resource competition and dispersal that are similar to the tabs just described for the target species, so example screens for these tabs will not be illustrated. For disturbance, plant functional type inputs are more detailed than for the target species inputs (interface illustrated below). This is because the plant functional types provide the vegetation structure for the simulation. More detailed information about response to disturbance, particularly fire, is required to adequately simulate vegetation structure. Plant functional type response to fire is defined for multiple age classes and multiple severity of disturbance. Mortality due to different classes of fire can be defined. The number of individuals in a stratum in turn determines the intensity of fire. For instance, a canopy fire cannot be carried in a landscape with no mature (canopy) trees. The plant functional types therefore provide the structure in which target species range movement and disturbances operate in the simulation.

Figure 2.4.7. Disturbance (Plant Functional Type) tab.

21

2.5.　Parameter Requirements

Parameters are the information required to run a simulation. BioMove requires extensive information about target species and plant functional types. The majority of the required information can be gathered from the literature for well-known species. For rare species, estimates of parameters may have to be made, for instance from known responses in better-known relatives of the target species.

Parameterization of BioMove for several target species and plant functional types is described in the case studies presented later in this report. Settling on values for BioMove parameters is a very useful exercise for forcing resource managers and other users of the model results to be specific about the assumed behaviour of the species of interest and the systems in which they exist.

Among the parameters required for BioMove are target species life history parameters, such as number of years to reproductive maturity; fecundity - number of seeds produced; mortality in each age class; and disturbance response such as whether a species reproduces by seed or by resprouting after a fire. Many of these same parameters, but not all, are required for plant functional types. More detailed information on response to fire is required for plant functional types, for the reasons described above.

2.6.　Operating System Requirements

BioMove operates on any PC running Windows 2000 or above and with at least 5 gigabytes of disk space for file storage. If the time-series output is utilized, larger memory requirements may be necessary depending on extent size and time interval specified. The model can typically be implemented on a laptop computer, with simple runs taking several minutes and more complex runs (abundant species, large study area) requiring hours. Off-line written text for parameterization can be pasted into the command-prompt operation using the *Scheduler* function.

3.0   Model Applications

This section provides an overview of four unique applications for BioMove; threatened species assessment, management coordination and decision support, invasive species assessment and advance climate change studies.

3.1.   Threatened Species Assessment

One of the critical policy-relevant questions in climate change biology is the magnitude of extinction risk associated with climate change (Thomas et al. 2004). International policy uses ecological integrity as a benchmark (O'Neill & Oppenheimer 2002), yet international mechanisms for identifying threatened species have flagged only a tiny fraction of the species likely to be at risk of extinction due to climate change. Species threatened by climate change need to be identified for a wealth of other management and policy purposes, but species-level assessment for these purposes is also in its infancy. BioMove is uniquely positioned to improve this situation.

The United Nations Framework Convention on Climate Change (UNFCCC) of which the United States is a signatory, has as its goal "avoidance of dangerous anthropogenic interference with the climate system" (Markham 1996). "Dangerous" is in turned defined in terms of developmental, agricultural and nature conservation goals (O'Neill & Oppenheimer 2002). For nature conservation, the goal is to constrain climate change within limits that "allow ecosystems to adapt naturally". Extinction is one of the main consequences of failure of ecosystems to adapt to climate change, so assessing extinction risk has an important role to play in driving international policy (Lovejoy & Hannah 2005; Thomas et al. 2004).

The IUCN red list of threatened species is the main international vehicle for identifying species at risk of extinction (Commission 2001). To date, fewer than 2% of species on the red list have been identified as at risk due to climate change. National lists, such as the US endangered species listings, are not much further advanced (Bloomgarden 1995).

Existing extinction risk estimates are largely based on static, or 'envelope' species distribution models (Thomas et al. 2004). These models use present climate to calibrate a statistical model, then run the model with projected future climatologies generated by global climate models (General Circulation Models, GCM). The change in area of a species range between the present and the future can be used in conjunction with the Species Area Relationship (SAR) or Endemic Area Relationship (EAR) which simply state that fewer species exist in smaller areas, in a power law relationship that allows quantification of extinction risk (i.e., the number of species lost) (Kinzig & Harte 2000).

The problem with the species-area approach is that it can't speak to whether a species can attain newly suitable climatic space (Pearson 2006). The species distribution model can say where future suitable climate may be, but if that suitable climate space does not overlap or lie contiguous to current range, the model is mute on whether the species can reach that range. Dispersal ability and intervening land uses will govern attainment of

the newly suitable climatic space. To deal with this limitation in distribution models, studies of extinction risk typically assume two extreme outcomes that bracket the range of dispersal options: either the species can disperse perfectly to all suitable future climate space regardless of location, or that the species can only persist where current and future suitable climate overlap (Malcolm et al. 2005; Peterson et al. 2002; Thomas et al. 2004). In the literature, these are known as the 'perfect dispersal' and 'no dispersal' options. The issue is that reality lies somewhere in between these extremes and having a very low and a very high estimate leaves a large in-between area of high uncertainty.

BioMove is designed to exactly address the limitations of the species-area approach, and therefore can greatly improve and speed the process of listing species as threatened due to climate change. The attributes of BioMove that allow it to simulate the dispersal of a species to newly suitable habitat as climate changes are described above in the Model Description section.

The IUCN international red list process has now initiated a working group to help improve the listing of species threatened by climate change. This group is using combinations of species distribution models and population models. They anticipate a 3-5 year development process for this integrated modeling approach. This approach has some similarities to BioMove. While BioMove can model the spatial dynamics of populations seamlessly, the working group approach is still in the development stage, with many issues arising relating to transfer of information between the two model types they are attempting to join. This group will begin to test BioMove as an alternative next year, which may greatly speed the international red listing process for climate change.

Resource managers, national and regional threatened species authorities and others can use BioMove to greatly improve the process of assessing the extinction threat posed by climate change. Because BioMove explicitly simulates the processes that mediate a species transition from current suitable climate to future suitable climate, its ability to discriminate factors that may reduce extinction risk is much greater than other available methods. In BioMove, management options may be simulated and their effect measured, allowing informed choices between different approaches to saving species threatened by climate change and allowing significant savings where the costs of management interventions varies.

3.2.   Management Coordination and Decision Support

Site managers increasingly are realizing the need to factor climate change into current management decisions. Wildfires of greater frequency and intensity than historical norms are already affecting forest lands and protected areas throughout the US west, for instance (Brown et al. 2004; Westerling et al. 2006). Managers responsible for these areas are concerned that unprecedented climatic and disturbance regimes may push reserve ecosystems 'over-the-edge' into degraded states or states with no historical analog. To

better manage or prevent these system conversions, managers need research tailored to decision support (Brown et al. 2004).

BioMove is well-placed to provide a research tool that can fill the information needs of managers facing climate-driven changes in the systems they manage. BioMove incorporates disturbance modeling capability, which allows simulation of changed fire frequencies or intensities, one of the factors of greatest concern as climate changes, particularly in California (Westerling et al. 2003).

Equally importantly, BioMove can simulate how changed disturbance regimes interact with vegetation structure and composition. This allows the model to serve in support of decisions concerning management manipulations such as vegetation thinning or prescribed burning. The ability of the model to treat multiple disturbances, such as the effects of fire and grazing together, give it even greater versatility and management relevance.

Decision support using BioMove may be most effective where researchers and managers work together to parameterize and run the model. Because BioMove requires an extensive array of life history and disturbance response parameters, it is very good at forcing researchers or managers to be explicit about their assumptions about how a system functions. If researchers make parameter estimates, the opportunity to tap manager's knowledge of the system is lost, as is the ability for managers to use the model as a learning tool. When managers and researchers implement the model together, management assumptions about how species and disturbances operate are made explicit, and learning about the system by varying parameters and observing modeled responses is promoted.

Some management agencies have in-house research capacity that will allow easy adoption of BioMove. Many agencies will want to form partnerships with University research groups able to run BioMove to reduce in-house science needs and to allow the agency focus on management. Through these partnerships BioMove can be implemented in a decision support mode, in which managers are actively involved in choosing parameters and testing the effects of changes in model configuration.

Applications for which BioMove may have value in regional or site management include examining the impact of changing fire regimes on vegetation and species, examining the effect of changing species composition due to climate change on fire or air pollution, management of endangered species, anticipation of habitat needs of species of concern, land use planning for counties in which nature conservation is a long-term goal, and other timely management issues. Application to each one of these management challenges will require investments of time and staff resources, but repay management agencies with a better understanding of the future behavior of the systems they manage.

3.3. Invasive Species Modeling

Understanding invasive species behavior is one of the critical research agendas for climate change. From nature conservation to agriculture to forestry applications, the behavior of invasives in changed climates will have a large influence on system behavior. Modeling has been used to look at invasions globally (Ficetola et al. 2007; Richardson & Thuiller 2007), regionally (Parker-Allie et al. 2007) and in individual sites or for individual species (e.g. (Ficetola et al. 2007). These assessments have in common the use of relatively simple species distribution models which do not incorporate temporal or spatial dynamics.

BioMove allows the introduction of spatial and temporal dynamics into studies of alien invasions at all spatial scales. Local and regional studies are easily conducted in BioMove. An example is provided in the case studies below for *Bromus madritensis*, or cheatgrass, in California. The global scale is most challenging for BioMove because of computational issues, but use of very coarse grain can allow global simulations in BioMove. Simulations in BioMove at all scales can help resolve the temporal dynamics of invasive species spread and identify factors that may favor more rapid spread. These applications may include tracking spread of diseases, agricultural pests, ecosystem disruptors, and watershed-damaging species as climate changes.

3.4. Advanced Climate Change Research

BioMove provides a platform for advanced climate change studies far more refined than that provided by distribution modeling alone, and distinct from some other types of modeling, such as Dynamic Global Vegetation Modeling. BioMove provides species-denominated answers to dynamic questions. Many such research questions have had no or only marginally appropriate methods with which to be addressed until now. The breadth of these possible research applications will depend on the ingenuity of climate change biologists, but two examples will be offered here to illustrate the potential.

One example is the assessment of "overshoot" greenhouse gas stabilization policies. Current international climate policy has begun to address the issue of "overshoot" - the possibility that global greenhouse gas trajectories will exceed target levels for some time, then gradually decrease to meet the target (Huntingford & Lowe 2007). One reason for this is the greenhouse gas levels may already exceed the threshold for important physical changes, such as loss of all arctic sea ice, that are undesirable. To reach acceptable levels below current concentrations, a temporary exceedance of the desirable target may be inevitable, to be followed by a reduction to meet the target. The biological consequences of such a strategy are unknown, however. Putting species through two climate transitions may result in greater range loss than a single transition to a higher target. BioMove can test the effects of a double versus single transition on individual species. It can therefore help inform whether higher stabilization levels or "overshoot" are preferred policy strategies from the point of few of maintaining healthy ecosystems and conservation of biodiversity.

A second example is the development of more sophisticated models of species response to climate change. BioMove itself is an advanced hybrid model, but the field will continue to advance, and tomorrow's models will be built on the advances of the past few years. As one of the most advanced and nuanced climate change biology models available, BioMove will allow the exploration of additional routines to address poorly understood aspects of species response to climate change. The implementation of BioMove is particularly suitable for these types of applications, as other landscape and biogeographic models may be joined to BioMove in the Lamos interface. For example, a hydrology model could be added to BioMove to examine the interactive effects of vegetation and water availability in altered climates.

Because BioMove will be widely available, many researchers will be able to experiment with its capabilities and develop new applications. Here red listing, decision support, invasive species assessments and advanced research have been highlighted. Other applications can be expected which have not been anticipated in the development or testing process. The strength of BioMove will undoubtedly move the field ahead to more advanced questions, which more sophisticated models and more advanced versions of BioMove will be required to address. The speed and complexity of those advances will be one measure of the contributions of BioMove.

4.0   Simulation Examples

The following section provides several examples of BioMove applications. Within each section an introduction to the target species is provided as well as an explanation of extent selection, parameterization and results. Each case study explores a unique capability of BioMove. The first case study illustrates the potential for BioMove to model *Pinus lambertiana* (sugar pine) under several climate change scenarios with a fire disturbance and land-use mask. The second case study highlights the importance of long-distance dispersal in a case study with *Yucca brevifolia* (Joshua tree) as the target species. The third case study models the intra-community competition by integrating three plant functional types that fill various niches in the *Quercus douglasii* (blue oak) woodland mosaic habitats. Also using blue oaks as the target species, a fourth case study uses BioMove to simulate the dynamics of a "leading edge" under climate change where long-distance dispersal and inter-community competition limit species movement. The fifth case study highlights the applicability of BioMove to model an invasive species, *Bromus madritensis* (red brome).

4.1.   Dynamic Modeling of Sugar Pine, (*Pinus lambertiana)*, North-Central Sierra Nevada Mountains, California

4.1.1. Introduction

Pinus lambertiana (Sugar pine) is a characteristic mixed-conifer species found throughout the Cascade Mountains of Oregon, Sierra Nevada Mountains of California and Sierra San Pedro Martir in Baja California (Kinloch and Scheuner 1990). It is found at elevations ranging from near sea level up to 3,000 km in the Transverse and Peninsular ranges of Southern California. In California it is found throughout the western slopes of the Sierra Nevada, where mixed-conifer is bordered down slope by interior live oak woodlands. Over the past two decades, mortality rates have increased for *Abies* spp. and *Pinus* spp. while recruitment rates have not changed (van Mantgem and Stephenson 2007). This suggests a potential for species die back in this region. Mortality trends could be exacerbated if water limitations and drought stress continues under climate change (van Mantgem and Stephenson 2007).

In addition to its ecological role in mixed-conifer systems, *P. lambertiana* is highly valued as a timber species in California. Managing this commercially important species under climate change is particularly challenging in this region because of the complex "checkerboard" pattern of public and private land ownership. The future extent of this species will therefore be governed by bioclimatic limitations and the associated competition with other species as well as those threats posed by disparate land management practices.

This case study highlights BioMove's unique capability to model climate change impacts, disturbance and land use affects on species distribution. Decadal climate change envelopes were integrated to the model using the *scheduler* function. These envelopes impose new effects of climate on mortality and fecundity every 10 years

through 2080. The type of output generated from this case study has important application to management coordination and decision support, particularly in regions such as the Sierra Nevada that produce many of California's natural resources.

4.1.2. Methods

Species and Extent Selection

To predict where this species may be found in the future, the authors modeled shifts in *P. lambertiana* in the northern Sierra Nevada, California, in the context of climate change, competition with a neighboring plant functional type and dispersal constraints. They selected a study area that captures much of the "checkerboard" ownership but also contains *Quercus* habitat representing potential competition for *P. lambertiana* as the bioclimatic envelopes of these two species shift under climate change (Figure 4.1.1). In this region, *Quercus* habitat is dominated by *Q. wislizenii*, an evergreen, shade intolerant oak. The modeled future distribution for *Q. wislizenii* predicts an upslope movement (i.e. eastward) in the Sierra Nevada, suggesting a possible increased competition with *P. lambertiana*.
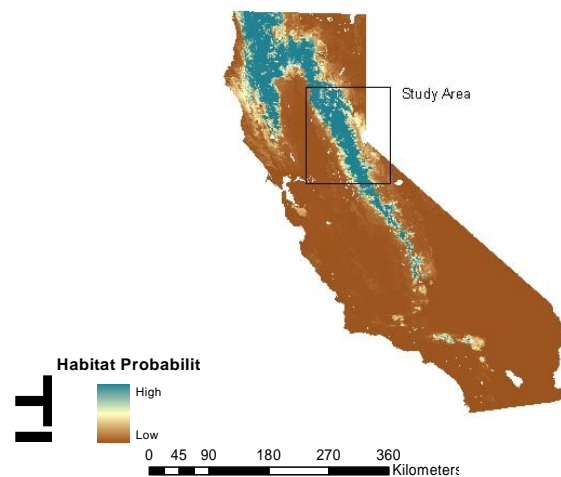
Figure 4.1.1. Modeled current distribution species occurrence for *Pinus lambertiana* in California.

Species parameterization

Input data (1 km) for Biomove included current and future *P. lambertiana* probability distributions derived from the BioMod technique (Thuiller 2003) based on species presence/absence and environmental data. Future climate data used in the future projections for probability distributions were based on the Hadley Centre (HADCM3) and Canadian Center (CCM) general circulation models for two IPCC greenhouse gas (GHG) emissions scenarios; A2 and B2 for the years 2050 and 2080. The greatest loss of *P. lambtertiana* distribution is predicted by the HADCM2 model with relatively consistent patterns between the A2 and B2 GHG scenarios (Figure 4.1.2). This loss is seen in lower elevation areas where as the CCM predicts little or no change in these down

slope areas. In contrast, the upslope areas are projected by the CCM to gain potential *P. lambertiana* habitat. Only minor increases in upslope habitat probability for the central region are predicted with the HADCM2.

A decadal time series of probability distributions was calculated by linearly interpolating from calculated future projections to generate a new envelope every 10 years. The model was run for 700 time steps (years) to reach equilibrium. The subsequent output was then used as the initial conditions for a simulation that included modeled bioclimatic envelopes every 10 years.
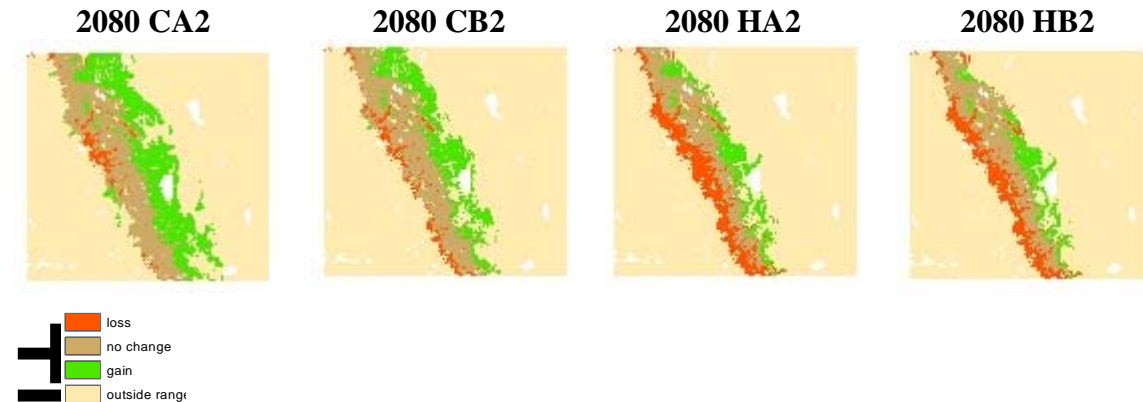
Figure 4.1.2. Modeled projected changes in species distribution for *Pinus lambertiana* for two GCMs (C; Canadian Center Model and H; Hadley Center Model). Each GCM was run using two sets of greenhouse gas emissions scenarios (A2 and B2).

The target species, *P. lambertiana*, was parameterized based on the current literature to explicitly define life history characteristics for each stratum (seedling, immature, mature, and senescent), mean and long-distance dispersal distances and response to competition with the plant functional type (Table 4.1.1). Age range for each stratum (Kinloch and Scheuner, Fowells and Shubert 1965), mortality (Kinloch and Scheuner, van Mantgem 2004), fecundity (Krugman and Jenkinson 1974) were derived or calculated from several sources in the literature. The maximum cell population was based on studies in the Sierra Nevada looking at pathogen and fire exclusion on demography. An estimate was determined based on values from the controls plots used in the experiment (van Mantgem et al. 2004).

Table 4.1.1. Demographic and physical parameters used to define target species, *Pinus lambertiana* in BioMove.

	Seedlings	Saplings	Mature	Senescent
Age range (years)	1 to 15	16 to 30	31 to 300	301 to 400
Annual mortality (%)	80%	20%	10%	3%
Effect of envelope (exponent)	1	0.5	0	0
Effective Fecundity (seeds/tree)	0	0	10	2
Physical Stratum	0	1	2	2
Max Cell Population (trees/km)	20,000			

Plant Functional Type Parameterization

An interior live oak plant functional type was selected due to its neighboring bioclimatic envelope and potential competition with *P. lambtertiana*. In this case, BioMove is used to look at inter-ecosystem competition as opposed to within ecosystem competition. Interior live oak, an evergreen oak is found in foothills, floodplains, valley bottoms and upland slopes up to 5,000 feet. Found throughout southern Klamath and southwestern Cascade ranges and on the western slope of the Sierra Nevada Mountains. Similar to *P. lambertiana*, it is also found scattered throughout the Transverse and Peninsular ranges of Southern California (Pavlick et al. 1991).

In Biomove, the plant functional type is parameterized similarly to the target species but with fewer specific parameters. For example, mortality is designated as yes/no for each age class at three light levels (low, medium, high) as opposed to a continuous function expression as used for the target species. In this regard, the plant functional type is not as explicitly characterized as a single species but allows for an agglomeration of species' to constitute a single plant functional type.

Disturbances

Fire is a dominant disturbance throughout the Sierra Nevada. Disparate fire management practices between public and private lands can lead to incongruent rates of ecosystem succession for neighboring parcels of mixed-conifer habitat. Fire suppression can pose threats to *P. lambertiana*, a relatively shade intolerant species (van Mantgem et al. 2004). As fire return intervals increase, the understory and leaf area index can increase shade and decrease the ability of *P. lambertiana* to successfully recruit.

To address the role of fire in this landscape, a submodule simulated fire and the effects on the target species and plant functional type. Five fire size classes were created (1, 4, 16, 64 and 256 km^2). Each fire size class was parameterized individually for its effect on the plant functional type and target species' mortality and ability to resprout. Fires were characterized using the "step contagion" fire sub-module in BioMove. This fire spread model works on a yearly time step although frequency of disturbance prone years and attempted fire starts per time step can be used to further define fire frequency.

Land use is also an important consideration for this region of the Sierra Nevada. Land ownership will influence management practices (e.g. harvest rates, planting regimes) thus affecting growth rates, reproduction and dispersal ability. In a separate simulation, the authors used a land ownership mask on the target species to differentiate public from private land holdings in the "checkerboard" region of the Sierra Nevada. The model was run for all public lands (including areas outside of the checkerboard for which the authors did not designate land ownership) while the private land was masked. This simulated privately owned timber harvest upon reaching maturity, limiting contributions to dispersal pools and not following regular recruitment patterns.

Simulation

The model ran using current distribution data for 700 years to reach a state of equilibrium for each model variable. Only the current envelopes were used for the target and plant functional types. These results were used as the initial conditions for the subsequent model runs which reloaded new bioclimatic envelopes every 10 years for the years between present and 2080. The model was then run for an additional 120 years with the 2080 bioclimatic envelope. First a simulation using the Hadley B2 scenario was run, with and without fire. Another simulation was run to compare the Hadley B2 scenario with an extreme scenario, the Canadian A2. A subsequent run used a land ownership mask on the Hadley B2 scenario.

4.1.3. Results

The HB2 scenario was used to test disturbance effects on mature abundance for the simulation with fire. There was little effect from fire on mature abundance (Figure 4.1.3). This is mainly attributed to the lack of spatial overlap between the plant functional type range and the target species range. Because only the plant functional type can 'bring' fire into a habitat, although it can affect both the plant functional type and target species, fires will only burn where the plant functional type is present. Therefore, there was no effect on the *P. lambertiana* from fire except in the marginal area where its range overlapped with the oak plant functional type. This region of overlap was not substantial enough to produce any effect from fire. Figure 4.1.4 is a matrix output display from the simulation with fire including target species' seedlings, immature, mature and senescent abundances, envelopes and plant functional type total abundance.

The abundance of mature individuals over time varied both in quantity and trajectory between the HB2 and CA2 scenarios (Figure 4.1.3). This is not surprising given the bioclimatic envelopes for *P. lambertiana* differ most between the retreating, downslope edges of the Hadley and Canadian. The differences between the GCMs are much greater than those between scenarios A2 and B2 (Figure 4.1.2).
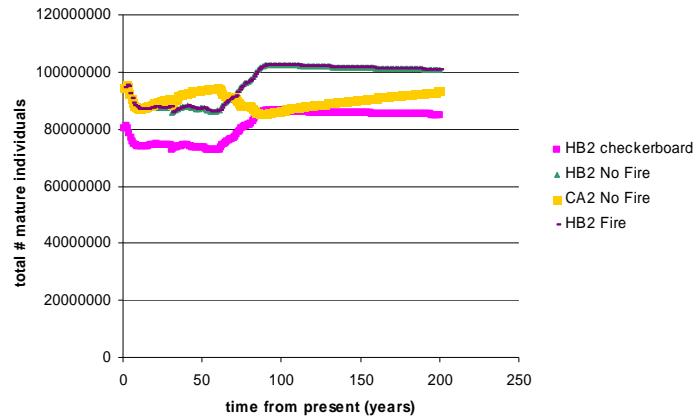
Figure 4.1.3 Number of total mature individuals for the entire study area across the 200 year simulation. Each line represents a different simulation. The HB2 (green) and CA2 (yellow) scenarios produce markedly different outputs. There was no difference between the runs with and without fire (purple and green overlapping lines), attributable to the lack of overlap between the plant functional type and target species habitat.
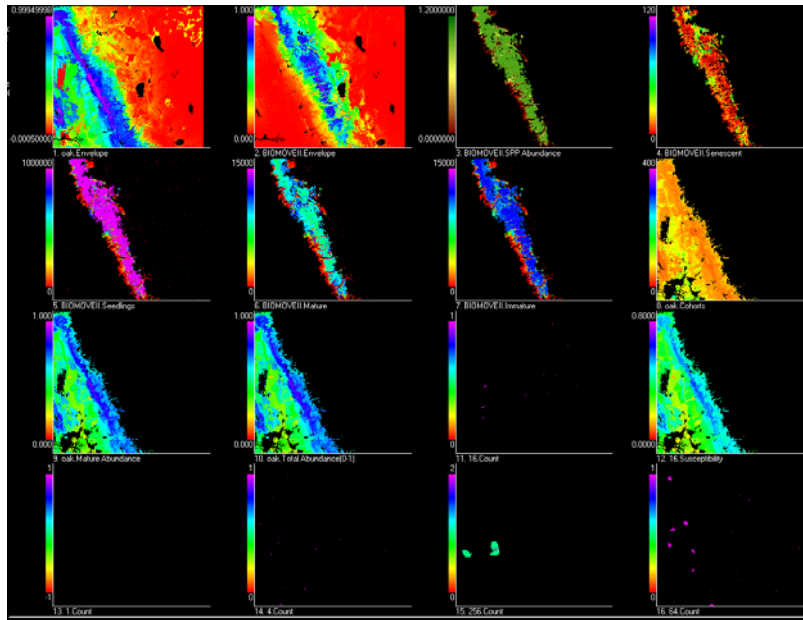
Figure 4.1.4. Matrix display of the HB2 (selected as an example) simulation with fire disturbance simulation (bottom row). Five fire size classes were used: 1, 4, 16, 64 and 256 km^2.

The land use mask reduced the total number of mature individuals. The mask blocked all dispersal into and out of the designated regions creating an overall depression in total number of trees (Figure 4.1.5).

(a)   **(b)**
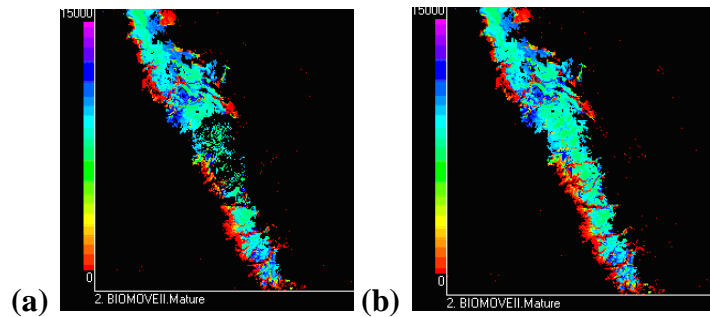
Figure 4.1.5 Total mature individuals for target species
***P. lambertiana* under two simulations; with a land**
ownership mask (a) and without (b).

4.1.4. Future Research

BioMove has been applied to a target species found in mixed-conifer ecosystems that bears similar life-history traits to other species in this ecosystem. However, it does not represent all members in this mixed-conifer community. An additional application of BioMove may be to examine intra-community competition with a functional type, instead of intra-community as illustrated with the *Quercus* plant functional type.

The role of fire in this study is a critical factor which warrants additional simulation. By including a plant functional type that provided intra-community competition, fire could be simulated within the mixed-conifer habitat. Fire in this simulation was confined to the neighboring communities defined by the *Querucs* plant functional type.

4.2. Dynamic Modeling of Joshua Tree (*Yucca brevifolia*), Mojave Desert of California

4.2.1. Introduction

The Joshua tree (*Yucca brevifolia*) is an iconic plant in the California Mojave desert, with a National Park and best-selling rock album among its many tributes. It is a long-lived, slow-growing, tree-like endemic desert perennial of the California Mojave desert (Hickman 1993, Turner 1982). It grows to 15m tall, has dark green leaves to 35 cm, 4-7 cm long flowers that are moth-pollinated, and inflorescence to 50cm. It produces a 15 cm fruit that is spongy that sheds seeds in August (Went 1948). The seeds are facultative, sprouting after a rain and have been shown to be dispersed by mammals. The species is found between 500 and 2000 m in the California Mojave Desert, in southwest Utah and in western Arizona. Its leaves have been shown to be tolerant of temperatures as high as 59^0C (Smith et al. 1983). Measured dispersal of seeds is limited, with maximum measured distance of 251 m (Lenz 2001). Considerable research over the years has led to a well-documented review of the species (http://www.fs.fed.us/database/feis/plants/tree/yucbre/all.html).

Studies on the sensitivity of Joshua tree to fire have varied in their results, with some indicating the capacity to resprout (Gorder et al. 2005) and others that the trees die upon burning (Brooks and Berry 1999). However, the vegetation types of the Mojave Desert are generally agreed to have very low natural fire frequency, and this has been altered

35

through the arrival of invasive annual species, particularly Bromes (*Bromus madritensis* subsp. *rubens* and *B. tectorum*), which are capable of carrying fire in these ecosytems (Emming 2005). These species increase the fire frequency, which in turn drives mortality of native species (Brooks and Esque 2002, Brooks et al. 2004). The fate of Joshua tree may be closely tied to its ability to disperse seed over long distances and its ability to compete with invasive species in the context of changing fire regimes. It is important to consider all of these variables when modeling the future distribution of Joshua tree.

BioMove is an ideal platform for modeling such a complicated system due to its ability to define short-lived invasive species in the demography model, simulate fire and allow for long distance dispersal. The objective of this BioMove run was to model the response of *Y. brevifolia* to changing climate conditions, and to examine the potential impact of invasive species on *Y. brevifolia* through its interaction with a plant functional type.

4.2.2. Methods

Input data (1 km) for BioMove included current (Figure 4.2.1) and future *Y. brevifolia* probability distributions derived from the BioMod technique (Thuiller 2003) based on species presence/absence and environmental data. Future climate data used for creating future species distribution projections were based on the Hadley Centre (HADCM3) and Canadian Center (CCM) global circulation models for two IPCC greenhouse gas emissions scenarios; A2 and B2, for the years 2050 and 2080. Environmental predictor weightings for future species distributions were derived from the present species distribution model and applied to the futures scenarios. All species distribution models used were consensus approach models, in which model results from four approaches (GAM, GLM, ANN, GBM and CART) were input to a principal components analysis, and predictor variable weightings derived from the first axis components.

Different climate scenarios generally showed range contraction along the western edge of the range for *Y. brevifolia*; however, the Hadley Center scenarios had less impact than the two Canadian climate scenarios. Generally, the model results indicated more suitable habitat remained in California than model results from Dole et al. (2003), who modeled a double CO_2 scenario for Joshua tree across its whole range at 10 km scale, an order of magnitude coarser spatial resolution than the models presented here.

The Canadian A2 scenario was used as input to BioMove. A decadal time series of probability distributions was calculated by linear interpolation from modeled future species projections to generate a new environmental envelope for Joshua tree every 10 years, from 2000 to 2080. The 2000 *Y. brevifolia* envelope was input into BioMove, along with the demographic, dispersal, disturbance, competitive plant functional type, and competition parameters. BioMove was run for 300 time steps (years) to reach equilibrium. BioMove output from the initial conditions run was saved as an "initial conditions file" (filename.icd) which was then used as the initial conditions for a simulation that included modeled bioclimatic envelopes every 10 years, and which was run for 200 years.

To simulate fire effects BioMove ran with the fire module turned off, and then with the fire module turned on. When fire was turned on, it was assumed to cause high mortality in all age classes except mature individuals, for which a 50% mortality rate was assumed.
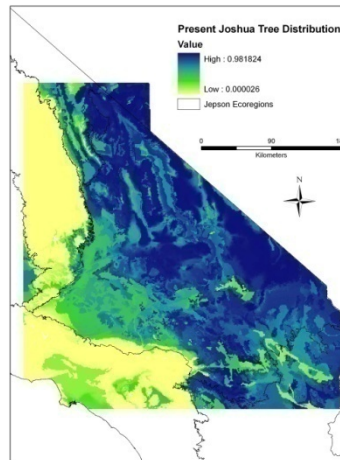
Figure 4.2.1. Current range suitability for _Yucca brevifolia_ as predicted from overlapping five BioMOD species distribution models.

Target Species Parameterization

The target species, _Y. brevifolia_, was parameterized based on the current literature to explicitly define life history characteristics for each stratum (seedling, immature, mature, and senescent), mean and long-distance dispersal distances and response to competition with the plant functional type (Table 4.2.1). The age structure was modified to reflect mortality in the second year, thereby permitting the functioning stage-based dynamics required of a matrix-based modeling approach such as BioMove. Age range, fecundity, mortality, and maximum population possible per 1 km^2 were derived from a variety of sources (see review: http://www.fs.fed.us/database/feis/plants/tree/yucbre/all.html).

Table 4.2.1. Demographic and physical parameters used to define target species, _Y. brevifolia_ in BioMove.

	Seedlings	Immature	Mature	Senescent
Age range (years)	0	15	30	150
Annual mortality (%)	N/A	70	5	80
Effect of envelope (exponent)	0.4	0.1	0.1	0.4
Effective Fecundity (seeds/plant)	0	0	150	2
Physical Stratum	0	1	2	2
Max Cell Population (individuals/km^2)	2,000			

Plant Functional Type Parameterization

Competition was modeled with a plant functional type (PFT) whose distribution is controlled by the combined envelopes for *Bromus madritensis* and *Erodium cicutarium* as modeled in BioMOD. These were selected to represent invasive annuals in the Mojave Desert. Inter-specific competition for light in BioMove is accomplished by specifying the slope and inflextion of a light response curve in addition to the allocation of different age classes to different strata. Joshua trees are not thought to have much competition for light, although the facultative nature of annual species seed sprouting suggests there might be competition for water after rains. However, the main possible interaction between the target Joshua tree, and the PFT used is that the PFT enables fire in these ecosystems and consequently increases the fire frequency.

Disturbance

Simulations were run both with and without a fire disturbance. When fire was included, it was with a constant 15 fires per year, with a maximum spread of 50 pixels (50 km^2).

4.2.3. Simulation

Using the present modeled distribution for the target species and plant functional type, a 200-year simulation without fire was run to bring the species distribution to equilibrium (Figure 4.4.4). Using the output generated from the spin-up, a 200-year simulation followed, starting with the current envelope at year 0 and applying the decadal climate envelopes in 2010, 2020, 2030, etc., up to 2080. The simulation ran for an additional 80 years using the 2080 scenario to see if the model outputs stabilized under the new climate values.

4.2.4. Results

When Joshua trees were assigned moderate dispersal capacity, BioMove indicated that the species would persist on the California landscape through climate change (Figure 4.2.2). This was true even with a moderate number of fires (Figure 4.2.3).

However, long-distance dispersal may prove to be an important constraint for this species. Figures 4.2.4 and 4.2.5 plot the difference in persistence of populations with moderate and low levels of dispersal. Figures 4.2.6 and 4.2.7 show the spatial result of two runs with low long-distance dispersal in conjunction with the same fire frequency used in Figure 4.2.6.
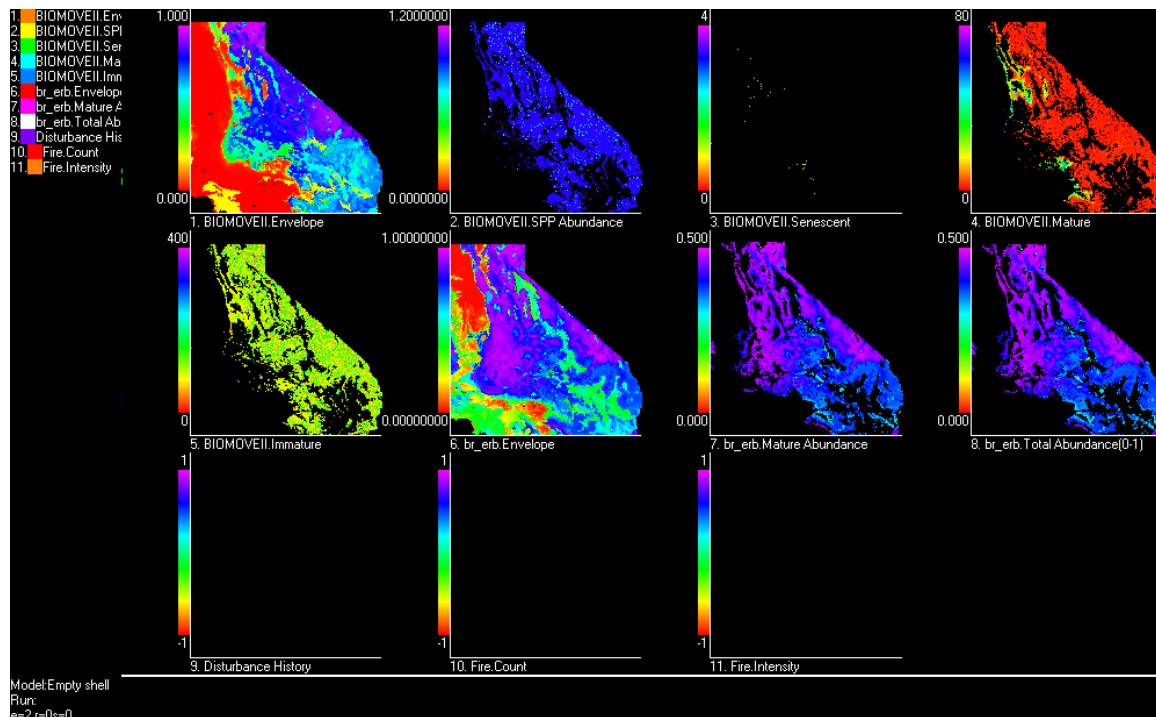
Figure 4.2.2. With moderate dispersal capacity, 2080 CA2 BioMove output for Joshua trees indicates persistence in the eastern part of the range (top row, center and left).
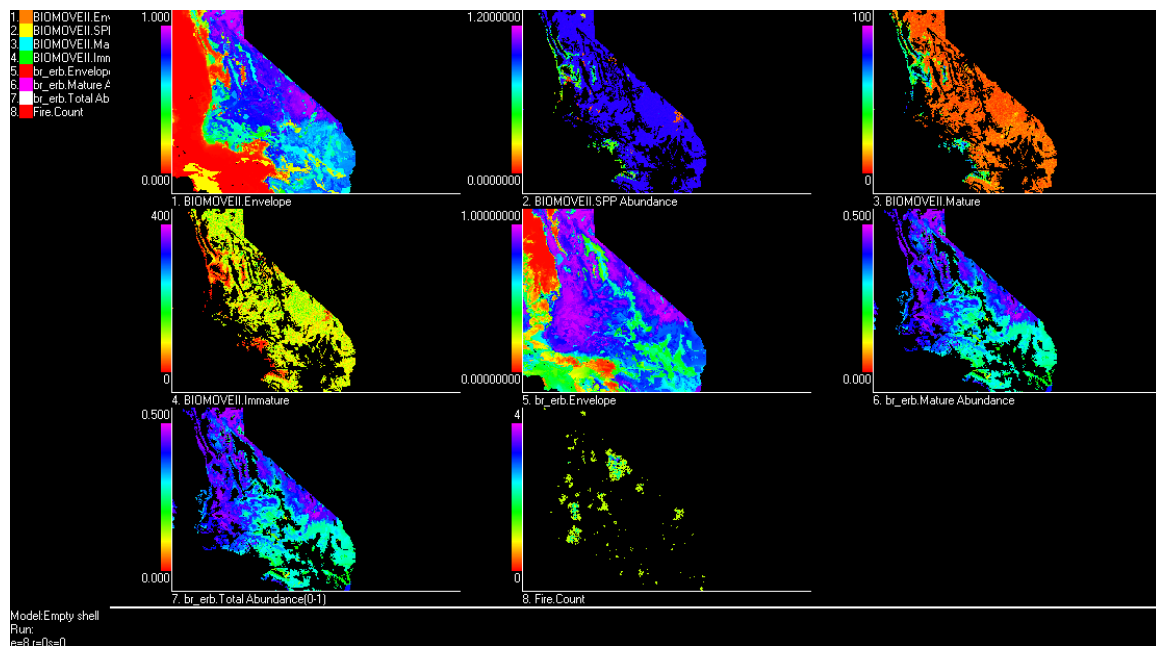
Figure 4.2.3. With moderate dispersal capacity and fire, 2080 CA2 BioMove output for Joshua trees indicates persistence in the eastern part of the range (top row, center and left). The fires shown in the last square are the cumulative fires on this landscape over the 200 years of the simulation. The plant functional type declines in abundance in the southern half of the range.

39
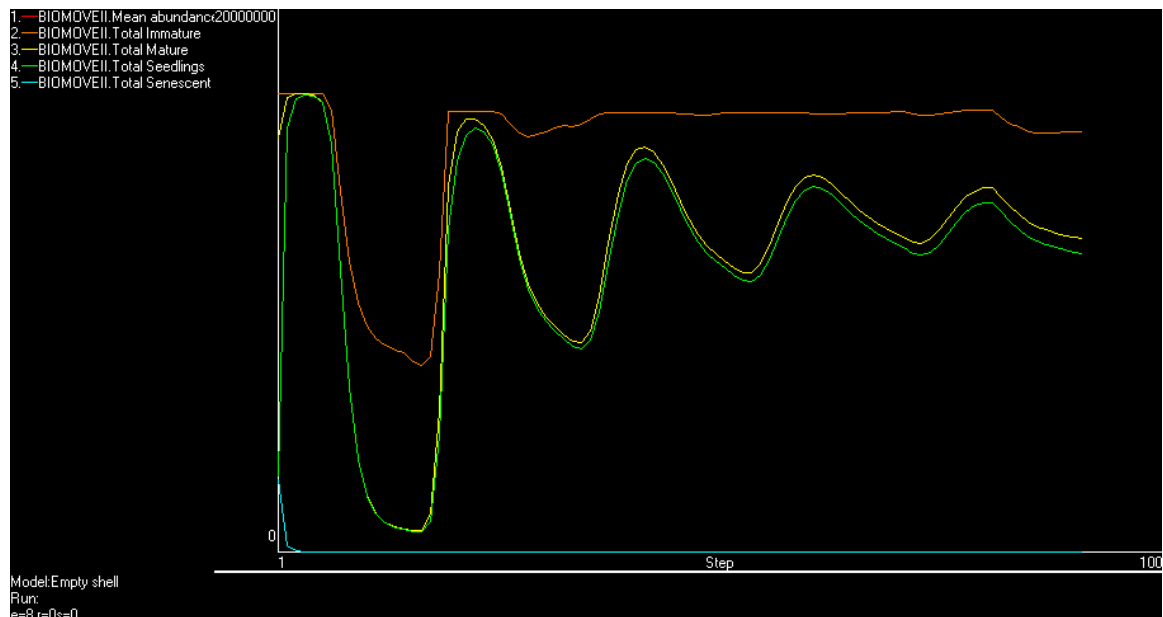
Figure 4.2.4. Population with moderate dispersal (2 pixel, 1% long-distance dispersal), showing progression towards a steady state population. Each line represents a different life stage: seedling (green), immature (orange), mature (yellow), and senescent (blue).
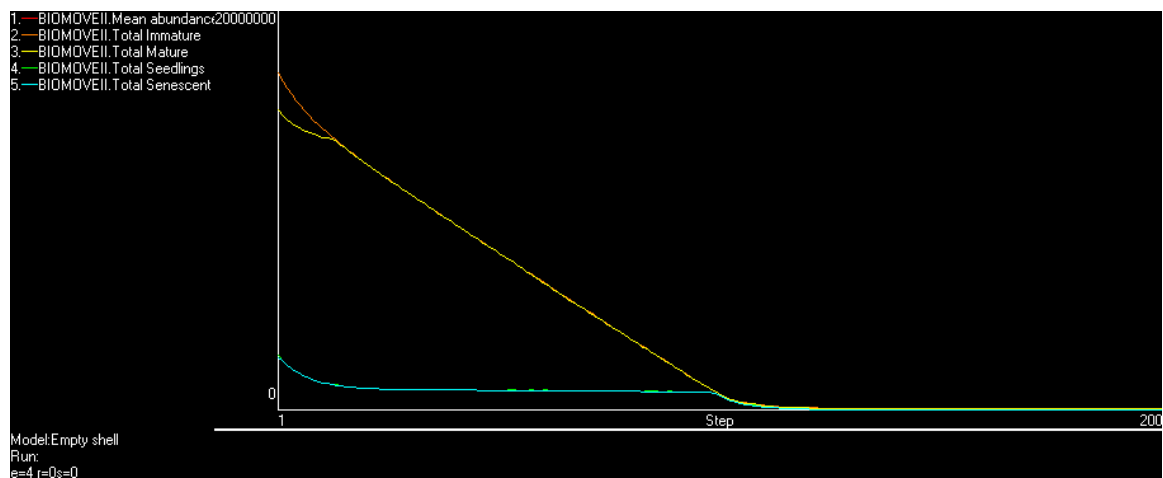
Figure 4.2.5. Population curve with limited dispersal (0.1% long-distance dispersal). This image shows the loss of the species within 100 years.
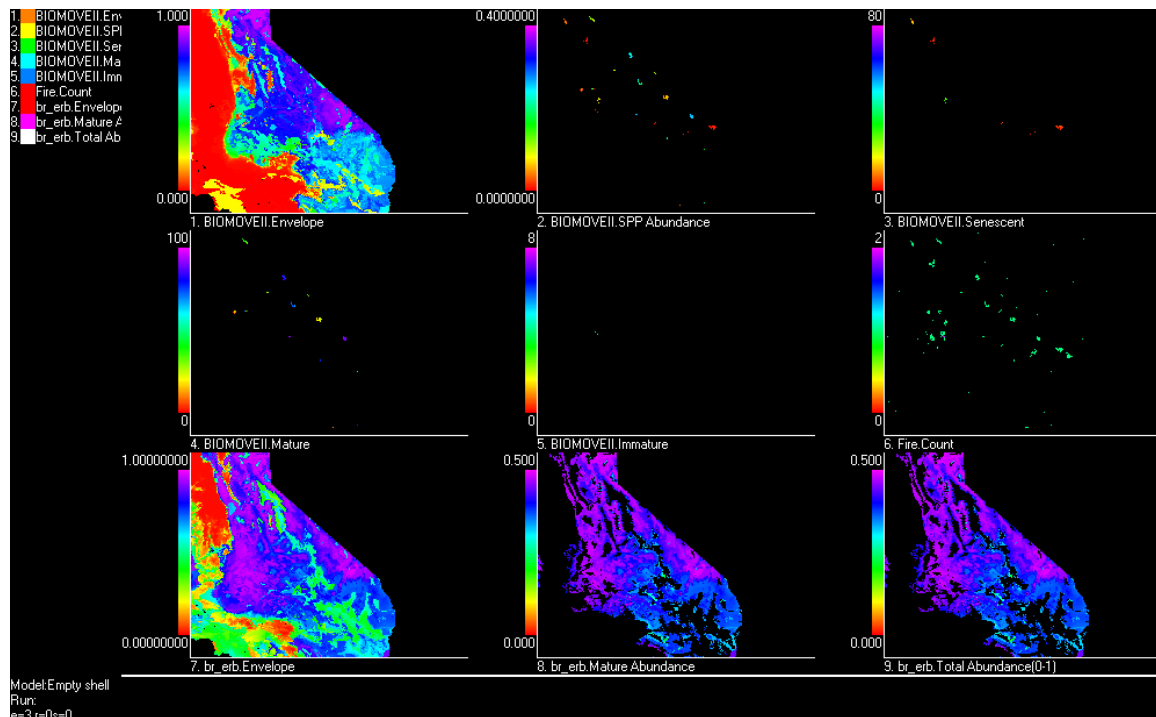
Figure 4.2.6. Low long-distance dispersal causes the loss of the species in California, represented by the few populations left seen in panels 2-4. Moderate fire was included in this model run (panel 5). Fire did but did not appear to extirpate the Joshua tree populations. The invasive plant functional type in the lower panels remained much the same as in the initial climate run.
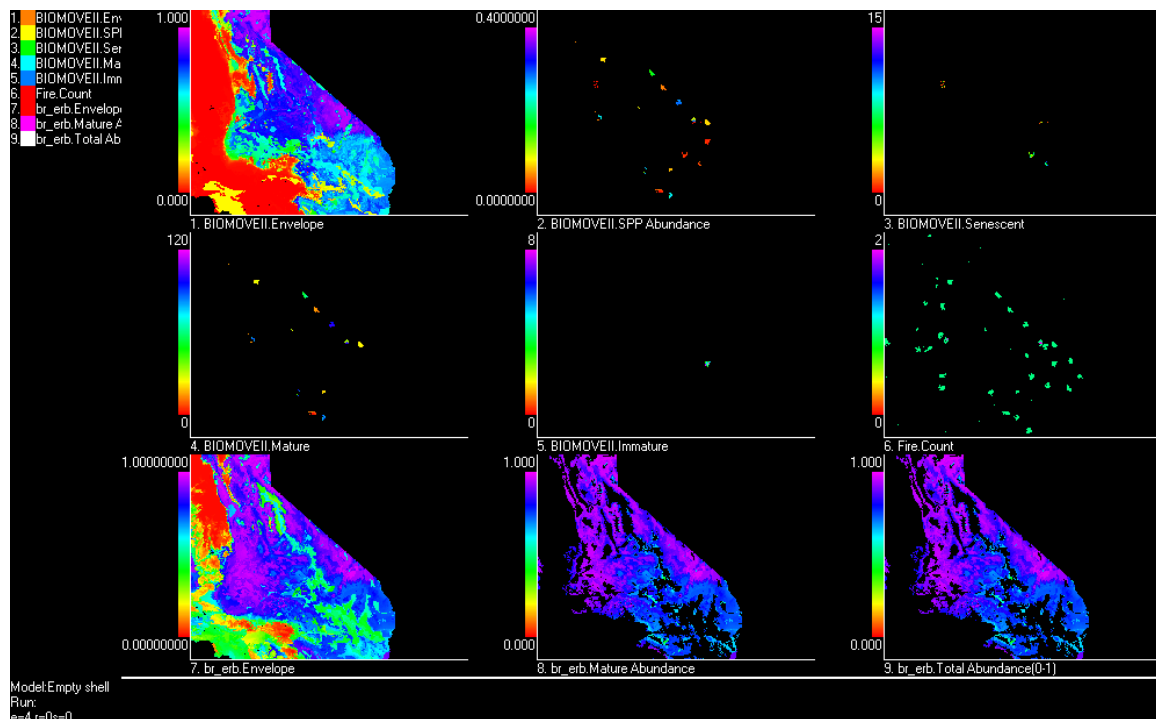
Figure 4.2.7. This shows another run of the BioMove model with Joshua trees configured with short long-distance dispersal.

4.2.5. Future Research

Long-distance dispersal capacity was a key variable in these model simulations. The literature suggests that the only known manner of dispersal for Joshua tree is via desert rodents (Vander Wall et al. 2006), although some Pleistocene megafauna have been speculated to have been dispersal agents. Long-distance dispersal events were set to equal 2 pixels, or 2 km. When these events occurred at a frequency of 1 per 1000 seeds, the population of Joshua trees declined to zero, regardless of whether there was fire. When the frequency of dispersal was increased to 1 per 100 seeds, the population of Joshua trees maintained itself, even in the event of fires. Even though some studies have been made of Joshua tree dispersal, the results of this modeling exercise suggest that more work is necessary to be confident of the long-term persistence of this important species.

Joshua tree populations tend to be spatially isolated. Genetic studies could potentially inform researchers about Joshua tree dispersal by quantifying the genetic distance (and estimated rates of genetic exchange) of existing isolated populations. Additionally, closer examination of the dispersal modes, potentially including wind- and bird-assisted dispersal experiments would be useful in determining how truly restricted the seed dispersal of the species is.

Joshua trees are potentially very long-lived species. This simulation ran for 200 years, but it is possible that runs of much longer periods of time would be necessary to effectively model the population dynamics of this species. How to handle the response of Joshua trees over periods relevant to their lifespans, when the climate projection models only go out 80 years is a challenge for the next round of research. This is compounded by the possibility that good recruitment years may be episodic and follow some combination of weather events that cause particularly good establishment conditions. Establishment for these plants is also slow, a phenomenon typical of many desert shrubs, and may take 100 years to establish (Guo 2004). Following grazing and other human disturbance, perennials in some North American deserts took over 50 years to re-establish (Guo 2004). This suggests that disturbance-initiated stand replacement could lead to vegetation type conversion. This dynamic also points to the importance of Joshua tree establishment period, something not explicitly modeled, but which likely combines rainfall, lack of fire, and successful competition with invasive annuals.

Along these lines, a possible model development challenge for BioMove would be the ability to include extreme rain events. Some studies suggest that Joshua trees have abundant seed production/recruitment in years of high rainfall. Since the annuals modeled also are facultative sprouters, competition for moisture in these years might play a pivotal role. This leads to another observation— competition in these systems may be related to root competition for moisture. BioMove currently models competition for light. In this system, the broadly spaced patterns of native shrubs means canopies are not closed (Went 1948). This suggests that the constraints of moisture have led to root competition. Shrub spatial patterns may be changing with incursion of annuals,

something that might be a good research area. From the perspective of future BioMove development, the recognition of different classes of competition may be a feature to consider for future addition.

4.3. Dynamic Modeling of Blue Oak (*Quercus douglasii*), Southern Coastal Mountains, California

4.3.1. Introduction

Blue oak woodlands are among the most diverse communities in North America, supporting more than 1,400 species of flowering plants, 29 species of amphibians and reptiles, 57 species of birds, and 10 species of mammals (Ritter 1998). Blue oak woodlands are found throughout the coastal ranges and the foothills of the Sierra Nevada in California. They are dominated by *Quercus douglasii* (blue oak) but also host valley oak, coast live oak, and black oak as well as many grass and shrub species in different portions of their range. Urban and sub-urban expansion, agriculture, and grazing threaten the persistence of blue oak woodlands. Climate change may exacerbate these current threats and must be considered when developing management strategies to help protect this unique community type endemic to California.

Although blue oak is a widely studied species in California (Borchert et al. 1989, Tyler et al. 2006, 2008), many questions remain regarding its patterns of recruitment. Some studies have indicated that populations of blue oaks may not be regenerating quickly enough to sustain a stable population. Absence of blue oak saplings and seedlings has been noted throughout much of the species' range (Bartolome et al. 2001; Bolsinger 1988; McClaran 1983). Regeneration is an area of concern in oak woodland conservation efforts, but the evidence tends to be contradictory and site-specific (Tyler et al. 2006).

Blue oak woodlands are unique in that they are found within a mosaic of grasslands, shrublands and forest communities. To comprehensively model how blue oak may dynamically change under climate change, it is important to consider competition with these other plant communities. If there is substantial competition for light with other species, blue oak could be outcompeted, particularly in areas where its bioclimatic envelope is less suitable for its persistence. Therefore, it is important to consider all of these communities when modeling BioMove in the face of climate change.

This application of BioMove utilizes the competition sub-model to simulate multiple levels of intra-community competition. BioMove is well-suited for this because it allows the user to define infinite plant functional types that can compete with the target species for a resource. The competition sub-model allows the user to designate different life stages to different strata, thus defining how much light is available to lower strata individuals. Additionally germination occurs at different rates according to light requirements and availability defined for both target species and the plant functional types. BioMove is particularly useful for modeling blue oaks in the southern coastal range because of its ability to integrate all plant functional types co-occurring with blue oak woodlands.

4.3.2. Methods

Extent and Plant Functional Type Selection

Blue oak is found throughout much of central California (Figure 4.3.1a). This particular extent was selected for simulation because of its highly heterogeneous pattern of plant communities within a relatively small geographic area. In this region of the southern coastal range, blue oak is found with perennial and annual grasses, sage scrublands, and chamise shrublands. Results from BioMOD using a principal components analysis predict loss of blue oak habitat for this portion of its range (Figure 4.3.1b).

(a)   (b)
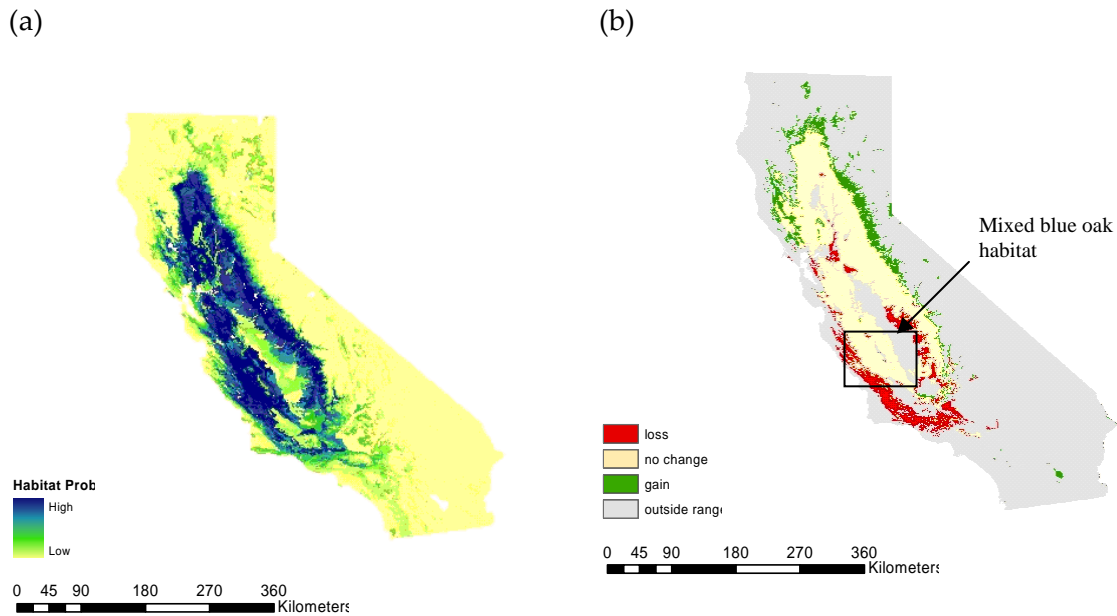
Figure 4.3.1: (a) Current predictions for current _Q. douglasii_ habitat probability (0-1) generated from BioMOD using principal components analysis. Low probabilities of occurrence are pictured in yellow and high probabilities in blue. (b) Changes (loss=red, no change=peach, gain=green) in habitat suitability for _Q. douglasii_ generated from the difference between current prediction of habitat suitability and future 2080 projected habitat suitability for the Hadley B2 scenario. The boxed region used in this study is comprised of mixed coastal sage scrub, grassland, and blue oak woodland.

Two plant functional types (PFTs) were used for the competition submodule. The shrub PFT was constructed by calculating the maximum of the presences of two shrub species, _Artemisia californica_ (California sagebrush) and _Adenostoma fasciculatum_ (chamise). Both are shade-intolerant perennial shrubs with high fire and drought tolerance. Although _Artemisia californica_ is deciduous and _Adenostoma fasciculatum_ is evergreen, they were merged together as a single PFT for the purposes of this modeling exercise since BioMove does not address phenological patterns. The grass PFT used was a perennial native grass, represented by the distribution of _Nassella pulchra_.

Species Parameterization

Table 4.3.1 summarizes the key demographic and physical parameters used in the BioMove model of blue oaks.

Table 4.3.1: Demographic and physical parameters used in BioMove model of blue oaks.

	Seedlings	Immature Trees	Mature Trees	Senescent Trees
Age range (years)	1-7	8-30	31-300	301-400
Annual mortality (%)	50	5	0.3	3
Effect of envelope	Strong (exp=1.0)	Weak (exp=0.5)	None	None
Effective Fecundity (seeds/year)	0	0	4	4
Physical Stratum	0	1	2	2
Max Cell Population	50,000 (sum of all age classes)			

Blue oaks are a long-lived species with high seedling mortality and low adult mortality. Allen-Diaz and Bartolome (1992) found blue oak seedling mortality to be approximately 50% per year under natural field conditions. Swiecki et al. (1993) found adult mortality to be in the range of 2–4% per decade, equivalent to 0.22–0.45% per year, so an intermediate value of 0.3% per year is used here. Fewer data are available for seedling and sapling mortality, but the sapling mortality of 5% used here is taken simply as a mid-range value between seedling and mature mortality rates. The rate of senescent mortality cannot be changed by the user but is calculated automatically in BioMove such that 95% of individuals die over the length of the age class.

The maximum abundance was chosen to produce a realistic density of reproductive individuals, comparable to dense oak woodland. Using a maximum abundance of 50,000 individuals per cell, the equilibrium age distribution on suitable habitat has between 5,500 and 7,000 reproductive (mature and senescent) individuals per km². This corresponds to a reproductive tree density of approximately one tree every 12-14 meters.

The effect of envelope values on mortality for the different age classes is based on the factors that are expected to control the current distribution of the species. The effect of climate on mature and senescent blue oaks is likely to be negligible, since they have deep tap roots that provide them with reliable sources of water. Likewise, the envelope has a very subtle effect on fecundity. The species distribution is likely driven by the mortality of seedlings and immature individuals, which are more strongly impacted by moisture availability near the surface. Thus the mortality of juveniles and sub-adults is affected by the climate envelope with a logarithmic type function, such that low envelope values are strongly affected by the envelope and high envelope values are less affected.

The effective fecundity (number of successfully-sprouting acorns per year) is 4 for both mature and senescent. This value was based on a rough calculation using measurements of average seedling recruitment and acorn production for blue oaks in Borchert et al. (1989). Seeds are dispersed randomly into the neighborhood of the parent grid cell according to an exponentially-weighted probability function. Dispersal occurs at both local and long-distance scales. Local dispersal accounts for 99.9% of all dispersal and has a mean "throw" distance of 10 m, which essentially restricts all local dispersal to the parent cell. The remaining 0.1% of dispersal is allocated to long-distance events, which have a maximum throw distance of 3 km, equivalent to a mean distance of 650 m.

4.3.3. Simulation

This BioMove simulation used the envelopes produced by the principal components analysis in BioMOD. This method uses a consensus method to identify those areas with highest individual model agreement for species abundance. Four scenarios (Hadley A2, B2 and Canadian A2 and B2) produced with BioMOD were used for bioclimatic envelopes and initials conditions. Starting with an initial distribution that followed the shape of the current envelope for blue oaks, the model ran a 500-year simulation to bring the species distribution to equilibrium. A 300-year simulation starting was run with the current envelope at year 0 and with new climate envelopes decadally between the present and 2080.

4.3.4. Results

Intra-community competition is an important aspect of dynamic species modeling when considering the potential threat of climate change on habitat suitable for species' persistence. Microclimatologies in this region are reflected by the heterogeneous pattern of species distribution in the southern coastal range. BioMove captures these dynamics through incorporating multiple plant functional types to compete with blue oak.

Blue oak was modeled for four future climate scenarios, C (Canadian) A2 and B2 and H (Hadley) A2 and B2. All of the simulations produce markedly different results for all variables. Figure 4.3.2 shows two selected variables, blue oak total seedlings and blue oak total mature individuals.
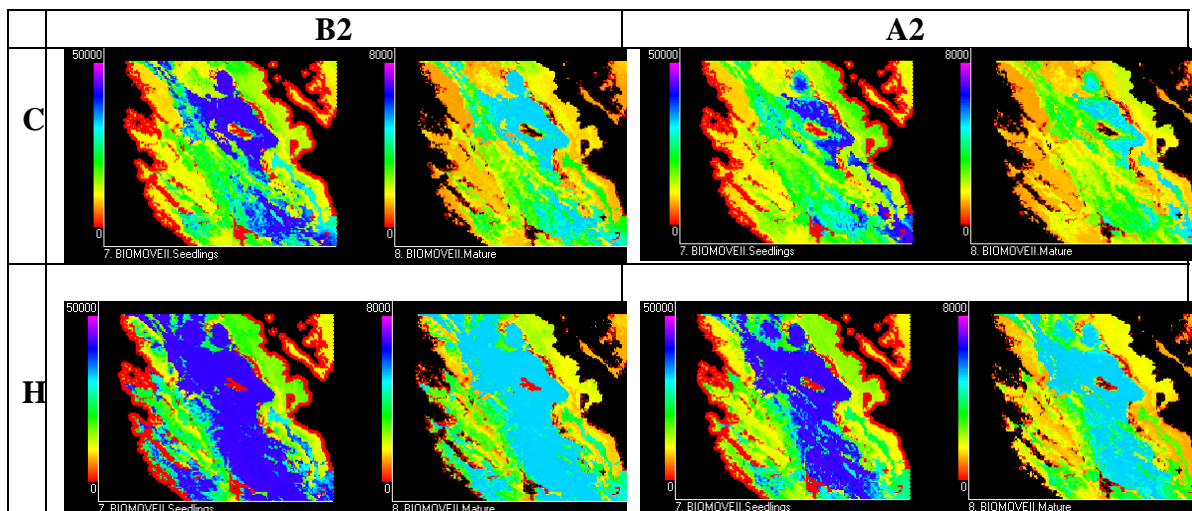
Figure 4.3.2. BioMove results for two climate change scenarios (B2, A2) and two GCMs (C=Canadian, H=Hadley). Each panel contains modeled abundances for two variable outputs, seedling (left) and mature (right) abundances. Numbers correspond to total number of individuals in entire study region.

The Hadley B2 simulation predicts the greatest number of seedling and mature blue oaks for the study region. The difference between the B2 and A2 simulations are slight but noticeable. The A2 simulation predicts lower abundances on the western slope of the coastal mountains. This pattern is exacerbated in both of the simulations using the Canadian model, which predict smaller abundances than either of the Hadley simulations.

4.3.5. Future Research

The geographical extent used in this blue oak case study is relatively small compared to the scale of potential microclimatologies that may affect the vegetation in this region. Coastal fog, inversion layers, and steep elevation gradients could all be causing regional scale climate patterns. This could be contributing to the distribution of species and the disturbances (e.g. fire) that may shape these distributions. Therefore, models that capture these smaller scale climatologies and are biologically relevant, should be considered when developing the species distribution models used as input in BioMove. Additionally, this area may face future urban development and conversion to agriculture. Local land use must be integrated into BioMove simulations if using modeling outputs to develop a management strategy for blue oak in this region

4.4. Dynamic Modeling of Blue Oak (*Quercus douglasii*), Northern Central Valley, California

4.4.1. Introduction

Blue oak (*Quercus douglasii*) is a widely-distributed California endemic species. Throughout its range, it is neighbored by different plant community types. In the northern portion of the blue oak range (Figure 4.4.1a), blue oak woodlands are neighbored at lower elevations by annual and perennial grasses and at higher elevations

by mixed conifers. Species distribution models predict northward movement under climate change.

This northern "leading edge" portion of its range where colonization of new habitat is taking place, is found in the northern portion of the Central Valley and the upslope margins of the western slope of the Sierra Nevada and the Coastal Range. The study region selected reflects the leading edge of the current distribution and includes the portion to which it is predicted to expand under the modeled climate change distributions (Figure 4.4.1b). In this area of its range, conspecifics maintain the population's ability to disperse into new areas provided they are able to overcome other competition and dispersal limitations.

Suburban and exurban development present some of the most immediate threats to blue oak woodland throughout California. Seventy-five percent of blue oak habitat falls under private ownership. While most of this land has traditionally been used for grazing livestock (Davis *et al.* 1998), ranching has become less profitable, and landowners have experienced increasing economic pressure to sell their lands for development. As oak woodlands are converted to agriculture or development, the remaining habitats continue to become highly fragmented. For this reason, the ability for blue oak to disperse possibly long distances over fragmented habitat, may become requisite for its persistence.

This simulation highlights BioMove's ability to simulate inter- and intra-community competition while taking into account long distance dispersal limitations. BioMove permits the dynamics associated with a "leading edge" of a species' distribution to be modeled in competition with co-occurring species as well as those species that pose competition in areas of colonization. These types of model outputs could have important applications for land management when designating new conservation areas under climate change.

4.4.2. Methods

Extent and Plant Functional Type Selection

Blue oak's leading edge, where colonization of new habitat is taking place, is found in the northern portion of the California's Central Valley. The study region selected for this case study reflects the leading edge of the current distribution and the portion to which it is predicted to expand under our modeled distributions under climate change (Figure 4.4.1b). Climate change over the coming century will drive the range of suitable habitats for blue oaks northward and upslope. Figure 4.4.1b shows the changes in blue oak habitat suitability generated from the difference between current range predictions and those for the 2080 Hadley B2 scenario. This future scenario is just one example of the projected habitat suitabilities produced with BioMOD. For this simulation, BioMove used the projected Canadian A2 and B2 future habitat suitabilities from BioMOD to model the dynamic response of blue oaks to climate change.
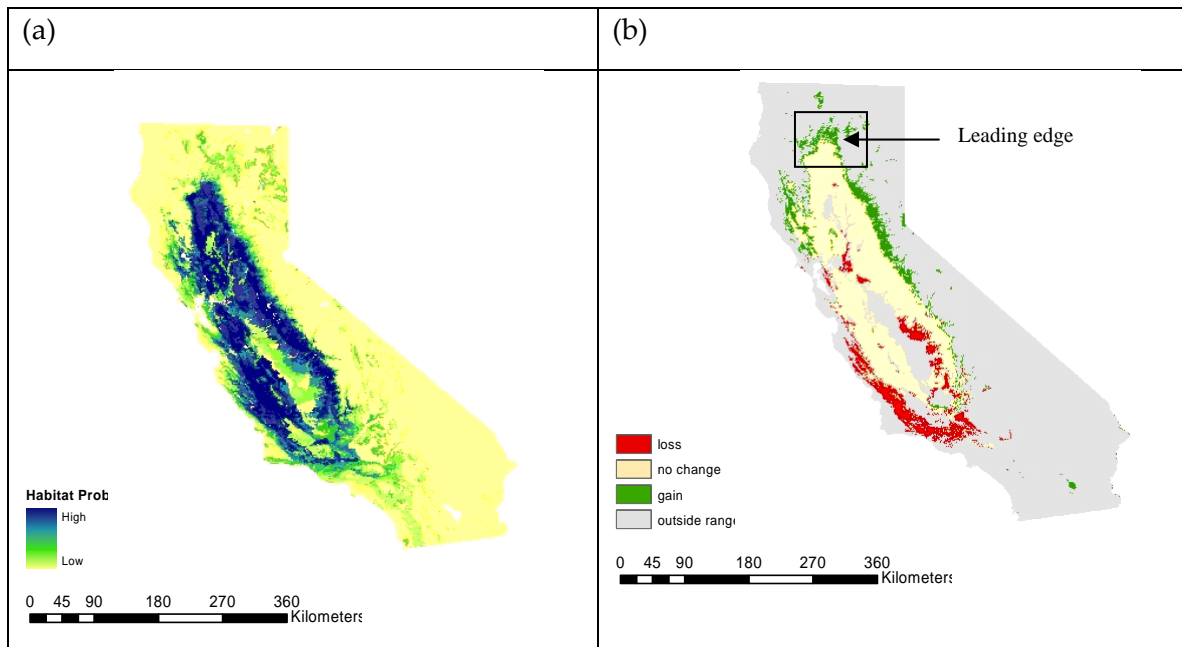
Figure 4.4.1: (a) Current predictions for Q. douglasii habitat probability (0-1) generated from BioMOD using principal components analysis. Low probabilities of occurrence are pictured in yellow and high probabilities are in blue. (b) Changes (loss=red, no change=peach, gain=green) in habitat suitability for Q. douglasii generated from the difference between current prediction of habitat suitability and future 2080 projected habitat suitability for the Hadley B2 scenario. The boxed region used in this study is the leading edge of the species distribution.

In this area of its range, conspecifics maintain the population's ability to disperse into new areas provided they are able to overcome other competition and dispersal limitations. Both competition with plant functional types (PFTs) and dispersal limitations present themselves as obstacles to blue oak persistence in this region. Three PFTs were used in the competition sub-model: shrub, grass, and pine. The shrub PFT was constructed by calculating the maximum of the presences of two shrub species, Artemisia californica (California sagebrush) and Adenostoma fasciculatum (chamise). Both are shade-intolerant perennial shrubs with high fire and drought tolerance. Although Artemisia californica is deciduous and Adenostoma fasciculatum is evergreen, they were merged together as a single PFT for the purposes of this modeling exercise since BioMove does not address phenological patterns. The grass PFT used was a perennial native grass, represented by the distribution of Nassella pulchra (purple needlegrass). A mixed-conifer PFT, represented by *Pinus lambertiana* (sugar pine), was also added to account for competition in upslope areas where blue oak may try to colonize under climate change,

Species Parameterization

Table 4.4.1 summarizes the key demographic and physical parameters used in the BioMove model of blue oaks.

Table 4.4.1: Demographic and physical parameters used in BioMove model of blue oaks.

	Seedlings	Immature Trees	Mature Trees	Senescent Trees
Age range (years)	1-7	8-30	31-300	301-400
Annual mortality (%)	50	5	0.3	3
Effect of envelope	Strong (exp=1.0)	Weak (exp=0.5)	None	None
Effective Fecundity (seeds/year)	0	0	4	4
Physical Stratum	0	1	2	2
Max Cell Population	50,000 (sum of all age classes)			

Blue oaks are a long-lived species with high seedling mortality and low adult mortality. Allen-Diaz and Bartolome (1992) found blue oak seedling mortality to be approximately 50% per year under natural field conditions. Swiecki et al. (1993) found adult mortality to be in the range of 2–4% per decade, equivalent to 0.22–0.45% per year, so an intermediate value of 0.3% per year is used here. Fewer data are available for seedling and sapling mortality, but the sapling mortality of 5% used here is taken simply as a mid-range value between seedling and mature mortality rates. The rate of senescent mortality cannot be changed by the user but is calculated automatically in BioMove such that 95% of individuals die over the length of the age class.

The effective fecundity (number of successfully-sprouting acorns per year) is 4 for both mature and senescent. This value was based on a rough calculation using measurements of average seedling recruitment and acorn production for blue oaks in Borchert et al. (1989). Seeds are dispersed randomly into the neighborhood of the parent grid cell according to an exponentially-weighted probability function. Dispersal occurs at both local and long-distance scales. Local dispersal accounts for 99.9% of all dispersal and has a mean "throw" distance of 10 m, which essentially restricts all local dispersal to the parent cell. The remaining 0.1% of dispersal is allocated to long-distance events, which have a maximum throw distance of 3 km, equivalent to a mean distance of 650 m.

The maximum abundance was chosen to produce a realistic density of reproductive individuals, comparable to dense oak woodland. Using a maximum abundance of 50,000 individuals per cell, the equilibrium age distribution on suitable habitat has between 5,500 and 7,000 reproductive (mature and senescent) individuals per km^2. This corresponds to a reproductive tree density of approximately one tree every 12-14 meters.

Regeneration of oaks is not fully understood despite the multitude of demographic studies. More recent literature studies have concluded reproduction may be a function of size rather than age (Tyler et al. 2006). Because age is difficult to determine for blue oak, individual size may be a more realistic parameter to define in modeling oak reproduction. A new demographic sub-module was developed that models the transition of individuals through time based on life stages as opposed to age. This allows

the user to define number of stage classes each with a corresponding probability of individuals staying in a stage class (e.g. juvenile, sub-adult, adult).

Simulation

The model was run for 500 years so that the target species and plant functional types could reach equilibrium. This was then used as the initial conditions file for the subsequent simulations. Envelopes for modeled habitat suitability were introduced on a decadal time step using the Scheduler function. The Canadian A2 scenario was used in all simulations. Long-distance dispersal was enabled for target species and all of the plant functional types.

4.4.3. Results

The top row of Figure 4.4.2 illustrates the initial bioclimatic envelopes used in the simulation. The blue oak target species, grass and shrub plant functional type all have highest probability of occurrence (blue/purple) in the central portion of the modeled extent. This corresponds to the northern limit of California's Central Valley. The pine plant functional type is found in the foothills surrounding the Central Valley (top row, right panel). The initial abundances of blue oak vary between life stages (middle row, 3 left panels).
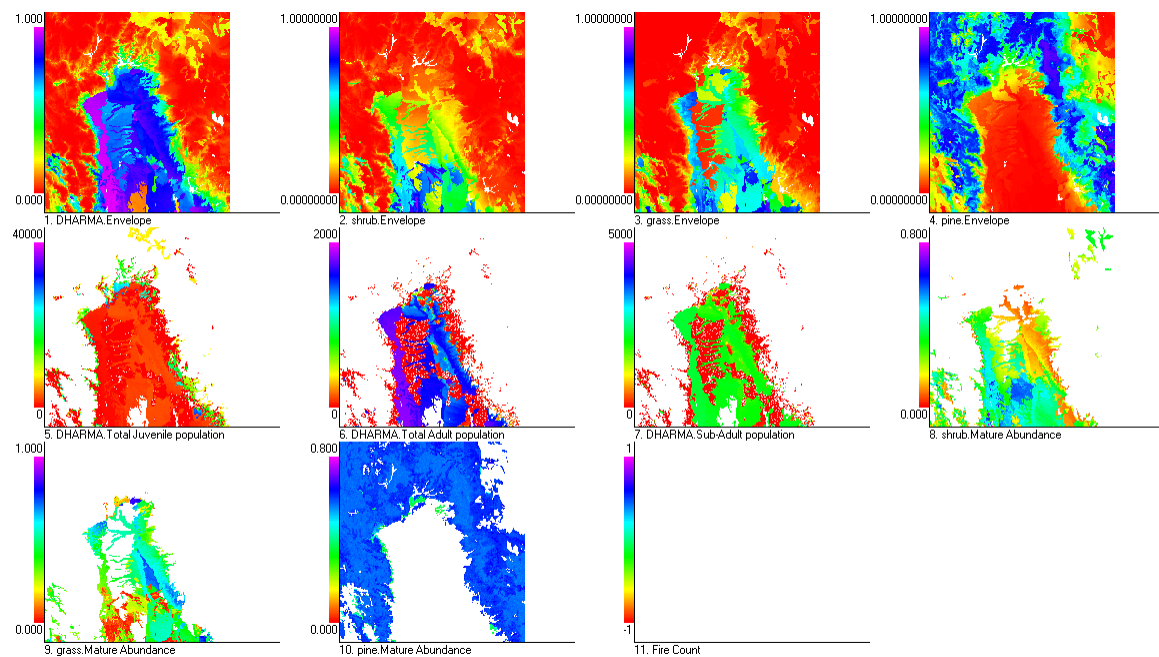
Figure 4.4.2. BioMove results at initiation of blue oak simulation. Envelopes used to designate habitat suitability for target species and three PFTs, shrub, grass, and pine are pictured in top row. Note that in this beta version of BioMove, the target species (blue oak in this case) is denoted "DHARMA."

The results show little success in the blue oak's ability to move upslope into the mixed-conifer habitat. There is some blue oak northward expansion of the leading edge as seen in the increasing distribution in each of the life stages. However, the abundances in these cells are very low, denoted by the red in the center row of panels (Figure 4.4.3) for the

51

year 2050. By 2080 (Figure 4.4.4), the abundances have decreased even more as illustrated by fewer cells with oaks present. This may be attributed to the competition with the shrub and grass plant functional types. Mature abundance for both the grass (middle row, right panel) and shrub (bottom row, left panel) plant functional types do not decline in the same proportions as the blue oak, as illustrated by higher probabilities of mature abundances (Figure 4.4.4).

Overall, there is little actualization of the potential niche in the leading edge of the blue oak. BioMove does predict movement into the bioclimatic envelope through long distance dispersal. However, the habitat suitability may be too low in this region to support oak recruitment, particularly in the context of competition with the pine PFT.
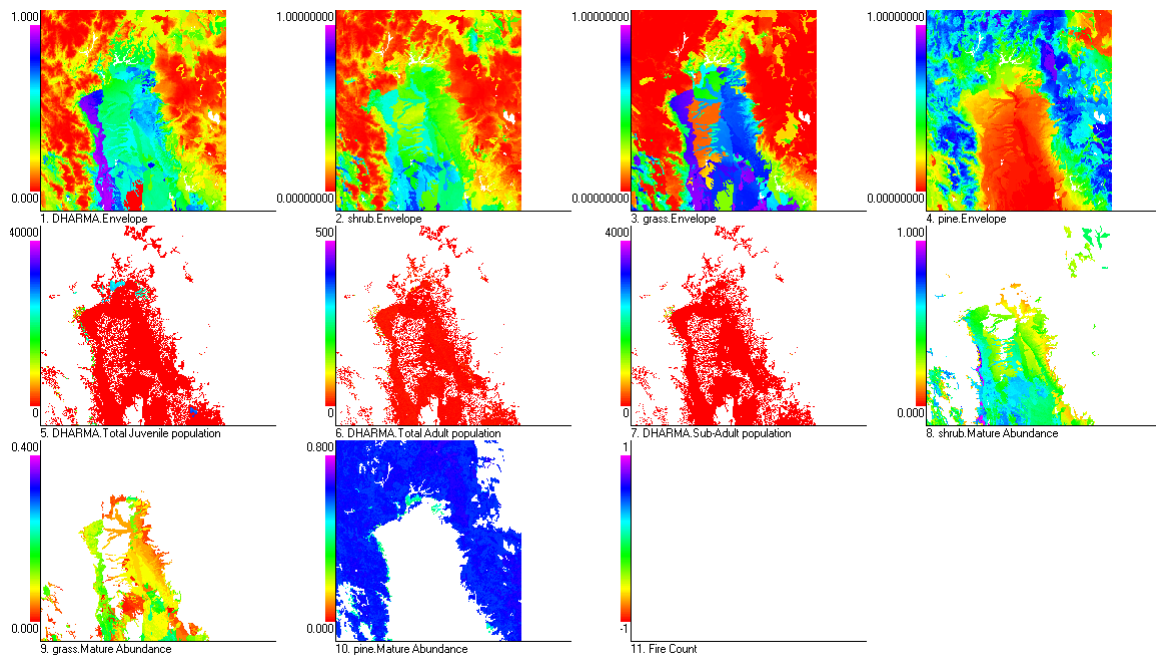
Figure 4.4.3. BioMove results for 50 years of simulation for blue oak. Envelopes used to designate habitat suitability for target species ("DHARMA"=blue oak), and three plant functional types, shrub, grass, and pine are pictured in top row.
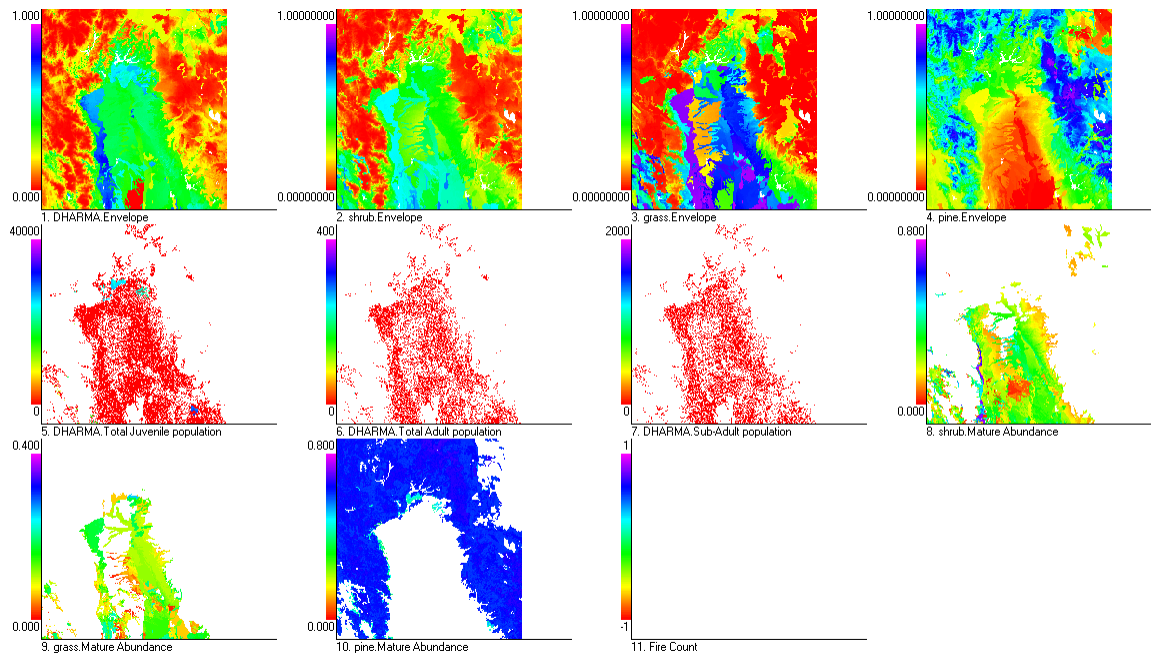
Figure 4.4.4. BioMove results for 80 years of simulation for blue oak. Envelopes used to designate habitat suitability for target species ("DHARMA"=blue oak) and three plant functional types, shrub, grass, and pine are pictured in top row.

4.4.4. Future Research

Recruitment and growth rate vary extensively in oaks and there seems to be little consensus in the literature. The values used in the juvenile mortality in this simulation were provisional values, chosen to allow a suitable population size at equilibrium. In an actual management application, variation of this variable would be a priority, to help define management assumptions and the sensitivity of outcomes to those assumptions. A sensitivity analysis of the demographic model would allow a more comprehensive definition of the growth and mortality values used. This highlights the importance of spatially explicit demographic studies to provide parameter data. The climate suitabilities in the simulation are a second critical factor in determining northward migration. Management actions could be informed by further exploration of the relationship between modeled climate suitability and actual abundances, a research priority for species distribution modeling and for this application of those models. Sensitivity analysis would also help to determine whether this is having a significant role in the blue ability's to migrate northward.

4.5. Dynamic Modeling of Red Brome (*Bromus madritensis*), North-Central Sierra Nevada Mountains, California

4.5.1. Introduction

Red brome [*Bromus madritensis* subsp. *rubens* (L.) Husn.] is an annual grass native to the Mediterranean region introduced to the western United States in the late 1800s (Hunter 1991, Beatley 1966, Salo 2005) and has widely invaded California. Red brome has the

53

capacity to convert vegetation in various ecoregions to grassland. It can impact both desert and chaparral ecosystems by affecting the fire frequency, which in turn drives mortality of native species, further facilitating its establishment (Brooks & Esque 2002, Keeley 2005). The species' current California distribution covers the Mojave and Sonoran deserts, the Central Valley, the coast ranges from Mexico to Napa and Lake counties, parts of the Modoc plateau and the western Sierra Nevada foothills (Figure 4.5.1).

Future climate change is expected to increase the range of red brome, with suitable habitats becoming available for invasion at higher elevations. This potential change could permit red brome to invade conifer systems, with potentially the same dynamic of increasing fire frequency coming into play in the conifer-dominated ecosystems of the Sierra Nevada (Keeley 2005). While the effects of such an increase of fire frequency are not known — would it lead to shift from conifer-dominated ecosytems to grasslands? — this modeling exercise attempts to illustrate the possible range of incursion of the grass into these systems.

This case study illustrates the application of BioMove to study the movement of an invasive species into an established ecosystem. Fire was used to create an avenue of establishment for the invasive species in the context of climate change, competition with a neighboring plant functional type and dispersal constraints. This simulation used the same extent used for the sugar pine (*Pinus lambertiana*) and oak (*Quercus spp.*) BioMove case study. The idea was to develop additional information for a concentrated region in the central and northern Sierra, which might permit the emergence of additional insights into the landscape-level dynamics of vegetation under climate change, and to create models which might also be further developed in later modeling efforts.
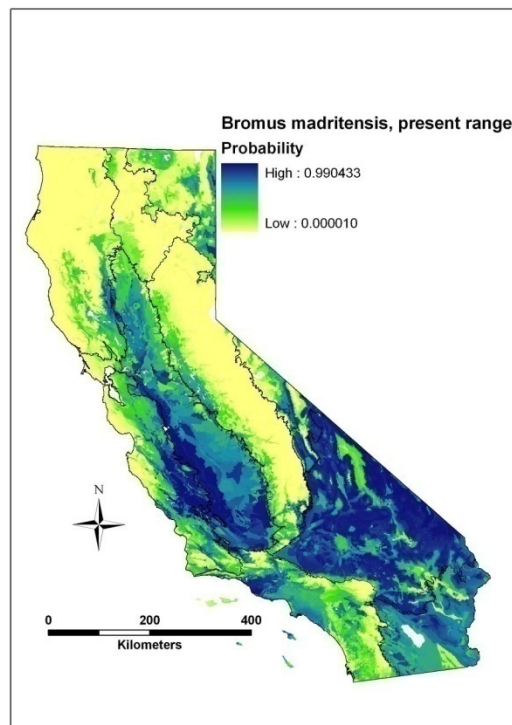
Figure 4.5.1: Current statewide *Bromus madritensis* range as determined by the overlap of predicted ranges from BioMOD using five different species distribution models year 2000 climate data.

4.5.2. Methods

Species Parameterization

Input data (1 km) for BioMove included current and future *B. madritensis* probability distributions derived from the BioMod technique (Thuiller 2003) based on species presence/absence and environmental data. Future climate data used for creating future species distribution projections were based on the Hadley Centre (HADCM3) and Canadian Center (CCM) global circulation models for two IPCC greenhouse gas (GHG) emissions scenarios; A2 and B2, for 2050 and 2080. Environmental predictor weightings for future species distributions were derived from the present species distribution model and applied to the futures scenarios. All species distribution models used were consensus approach models, in which model results from four approaches (GAM, GLM, ANN, GBM and CART) were input to a principal components analysis, and predictor variable weightings derived from the first axis components.

The current modeled and future HA2 scenarios were used for input to BioMove for this case study (Figure 4.5.2). A decadal time series of probability distributions was calculated by linear interpolation from modeled future species projections to generate a

new environmental envelope for *B. madritensis* every 10 years, from 2000 to 2080. The 2000 *B. madritensis* envelope was input into BioMove, along with demographic, dispersal, disturbance, competitive plant functional type, and competition parameters. BioMove ran for 300 time steps (years) to reach equilibrium. BioMove output from the initial conditions run was saved as an "initial conditions file" (filename.icd) which was then used as the initial conditions for a simulation that included modeled bioclimatic envelopes every 10 years, and which was run for 200 years.
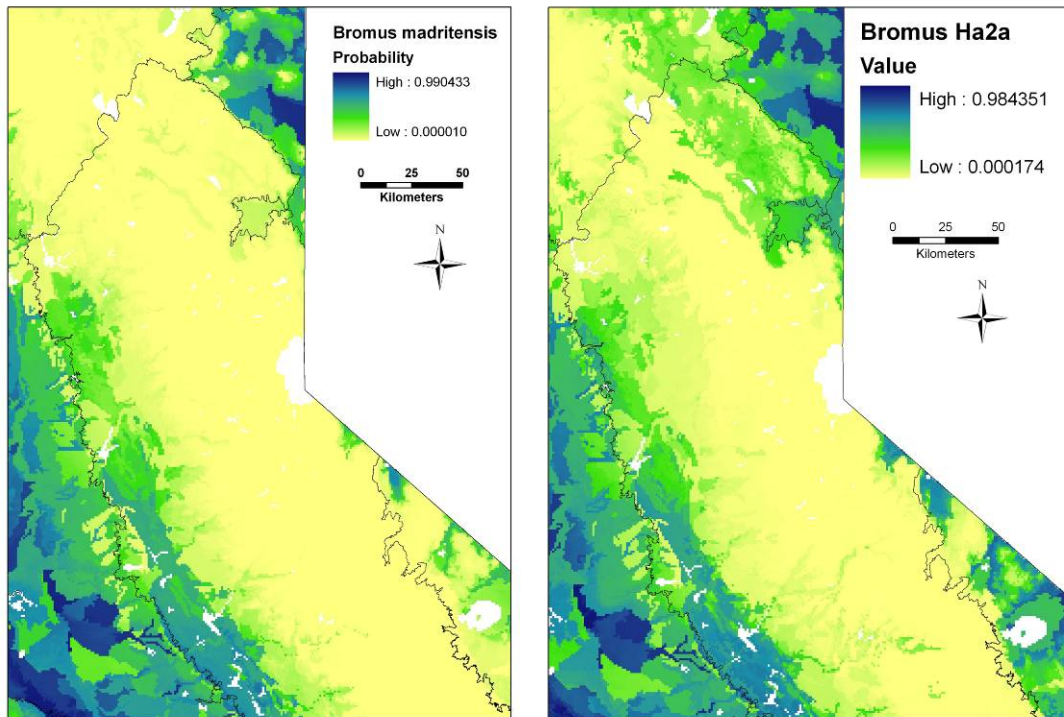
Figure 4.5.2. Detail of current and 2080 HA2 (for example) climate modeled range probability for *B. madritensis* in BioMove scenario study area. Green values indicate moderate saturation; upslope habitat gain is indicated on both sides of the Sierra Nevada.

Target Species Parameterization

The target species, *B. madritensis*, was parameterized based on the current literature to explicitly define life history characteristics for each stratum (seedling, immature, mature, and senescent), mean and long-distance dispersal distances and response to competition with the plant functional type (Table 4.5.1). Since *B. madritensis* is an annual, its age structure was adjusted to reflect mortality in the second year, thereby permitting the functioning stage-based dynamics required of a matrix-based modeling approach such as BioMove. Age range, fecundity, mortality, and maximum population possible per 1 km^2 were derived from a variety of sources, with review also covering the sister taxa *Bromus tectorum* (Huxman et al. 1999, Beckstead et al. 2007, Mack and Pike 1983, Norton et al. 2007, Pierson and Mack 1990, Rice and Mack 1991, Salo 2004, Salo 2005).

Table 4.5.1. Demographic and physical parameters used to define target species, *B. madritensis* in Biomove.

	Seedlings	Immature	Mature	Senescent
Age range	0	1	1	2
Annual mortality (%)	N/A	70	30	30
Effect of envelope (exponent)	0.5	0	0	0
Effective Fecundity (seeds/plant)	0	0	150	0
Physical Stratum	0	1	1	1
Max Cell Population (individuals/km^2)	150,000			

Plant Functional Type Parameterization

A mixed conifer plant functional type (PFT) was defined whose distribution is controlled by the envelope of Douglas fir (*Pseudotsuga menziesii*) as modeled in BioMOD, and represents the extent of the Sierra mixed coniferous forests. Inter-specific competition for light in BioMove was accomplished by specifying a response curve of the fir to light and the allocation of different age classes to different strata. The mixed conifer PFT impacted *B. madritensis* through shading, but was not impacted by the grass, excepting that the grass can establish more quickly, and promotes fire that could kill seedlings. It is possible that the grass' upper-elevation range limit is governed partly by competition with conifers. It is also possible that grasses will manage to invade mixed coniferous ecosystems in a manner similar to their successful establishment in desert shrub and chaparral systems in Southern California.

Disturbance

Two fire scenarios were modeled. First, 30 fire starts per year were modeled, with a maximum area disturbance of 50 km². Second, 10 crown fires were set to occur every fourth year. The two scenarios were set to see if *B. madritensis* would establish if mixed conifer forest areas burned and served as additional invasion sites.

4.5.3. Simulation

The model ran with no fire for 600 years to bring the species distribution to equilibrium. Using the output from the initial run, the model ran a 200-year simulation starting with the current envelope at year 0 and applying the decadal climate envelopes in 2010, 2020, 2030, etc… up to 2080. The simulation continued for 120 years using the 2080 scenario.

4.5.4. Results

The BioMove models show a general upslope establishment of the target species (*B. madritensis*) and considerable narrowing of elevational distribution of plant functional type mixed conifer forest, simulated by the range of Douglas fir (Figure 4.5.3). This pattern held true whether fire was permitted to burn in the simulations. Since the mixed coniferous forest and the grass range distributions were adjacent to each other, with the grass at lower elevation, the default scenario essentially showed the influence of climate.

Competition between the large trees and grass played out as limiting grass recruitment upslope from the range it occupied.

Long-distance dispersal varied between 4 and 10 km for the grass and had a probability of dispersal from 0.0001 to 0.01. The longer the distance and the more frequent the dispersal events, the more the background landscape of the mixed coniferous forest elevations were sprinkled with small populations of the grass (Figures 4.5.4 and 4.5.5).

Addition of crown fires led to loss of the majority of the Douglass fir within its band- the large mature stands were burned out. However, establishment of the grass in these open areas was limited- even when long distance dispersal was increased from a base case of 4km to 10km, when the influence of the climate envelope was minimized, and with a long-distance dispersal probability of 0.0001. When conditions for invasion were pushed to highly favorable for the grass (long-distance dispersal occurring for 1 in every 100 seeds, large crown fires, and low influence of environmental envelopes on the grass), presence of *B. madritensis* was broadly distributed in the mixed coniferous zone (Figure 4.5.6). This was evident as a large swath of new populations established itself further upslope on the west side of the Sierras, a phenomenon not evident in the runs where crown fires were restricted, and the climate envelope of the grass had a higher effect on the mortality of the grass.
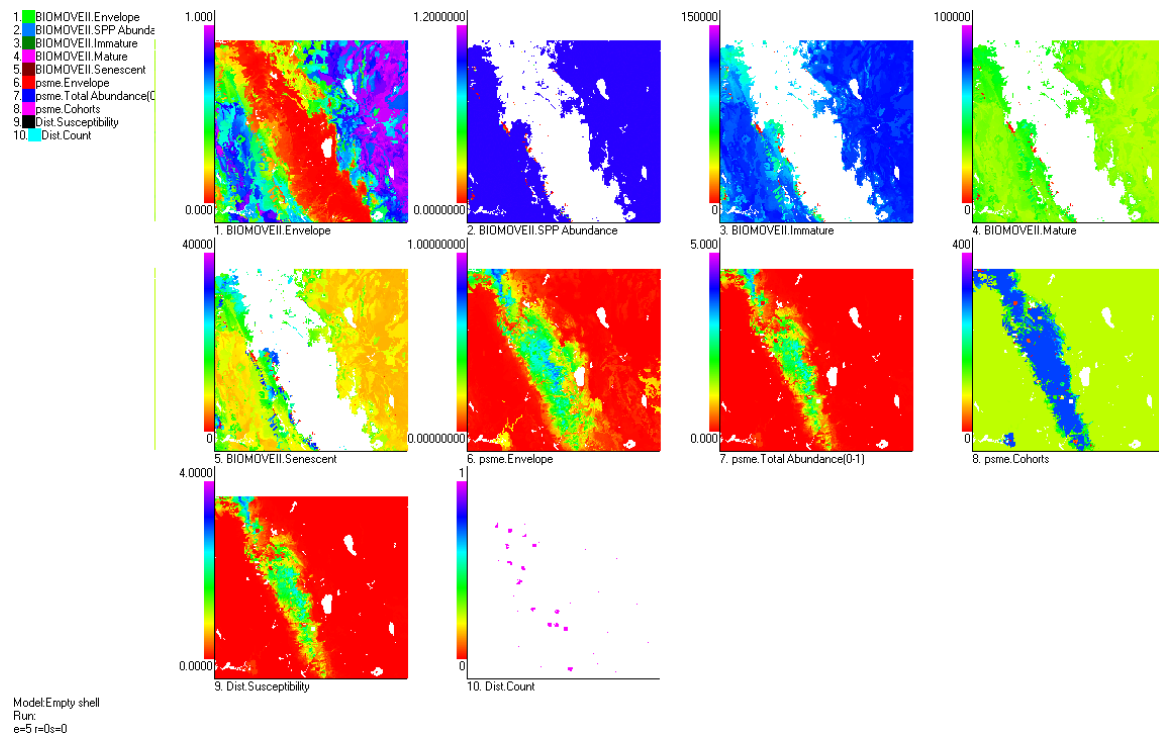
Figure 4.5.3. *B. madritensis* **moved upslope during the 200-year run, and the 80 years of climate change. The mixed-conifer plant functional type narrowed in extent and is much less abundant, as seen in 7a, middle row, third box being with green as highest abundance value rather than blue in the spin up run. New red brome populations establish along the upper edges of its suitable habitat range. Note that in this beta version, the target species is denoted by "BioMoveII" and the conifer plant functional type "psme."**

58
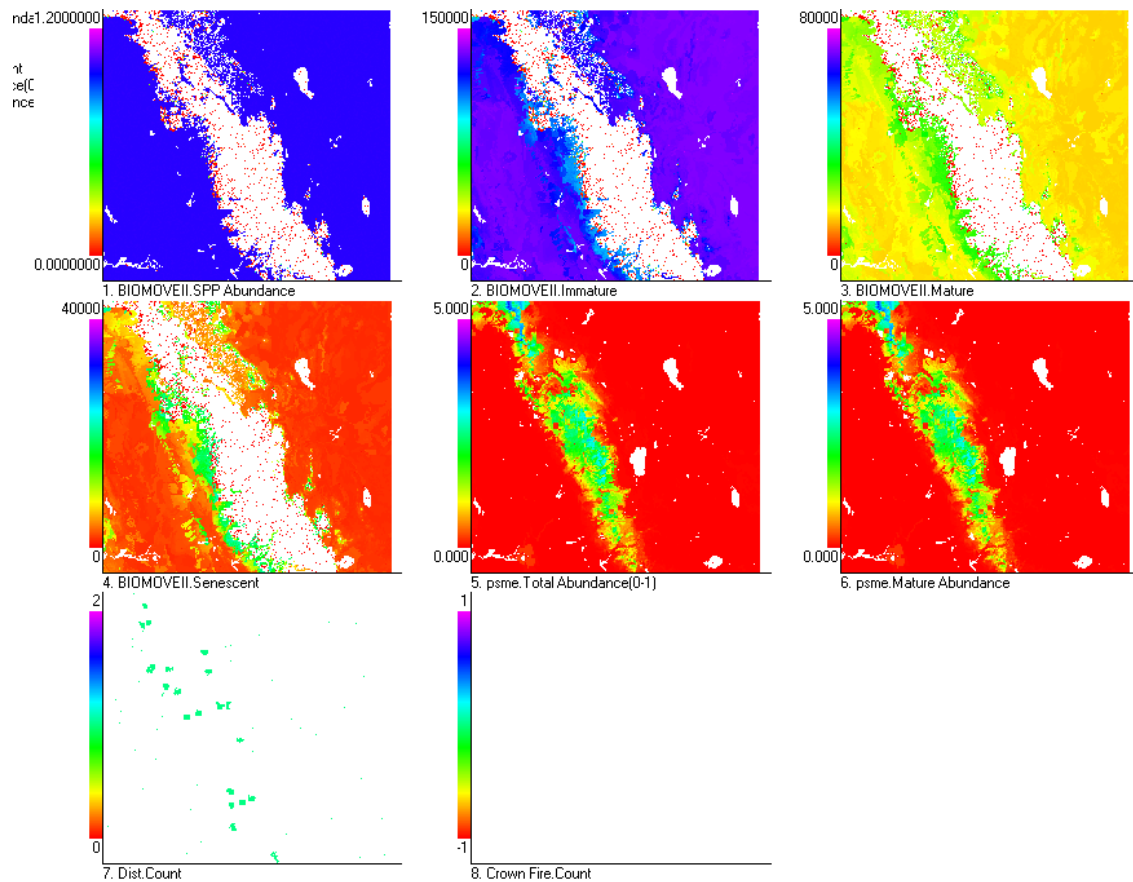
Figure 4.5.4. No crown fires, 0.01% seed long-distance dispersal ability, 4-km dispersal range. The conifer plant functional type ("psme") is narrowed. Populations of the invasive grass target species (denoted "BioMoveII") are visible throughout the region, even though the environmental conditions may be unfavorable. However, the large number of senescent populations of the target species (middle row, left box) indicates that these may not persist.
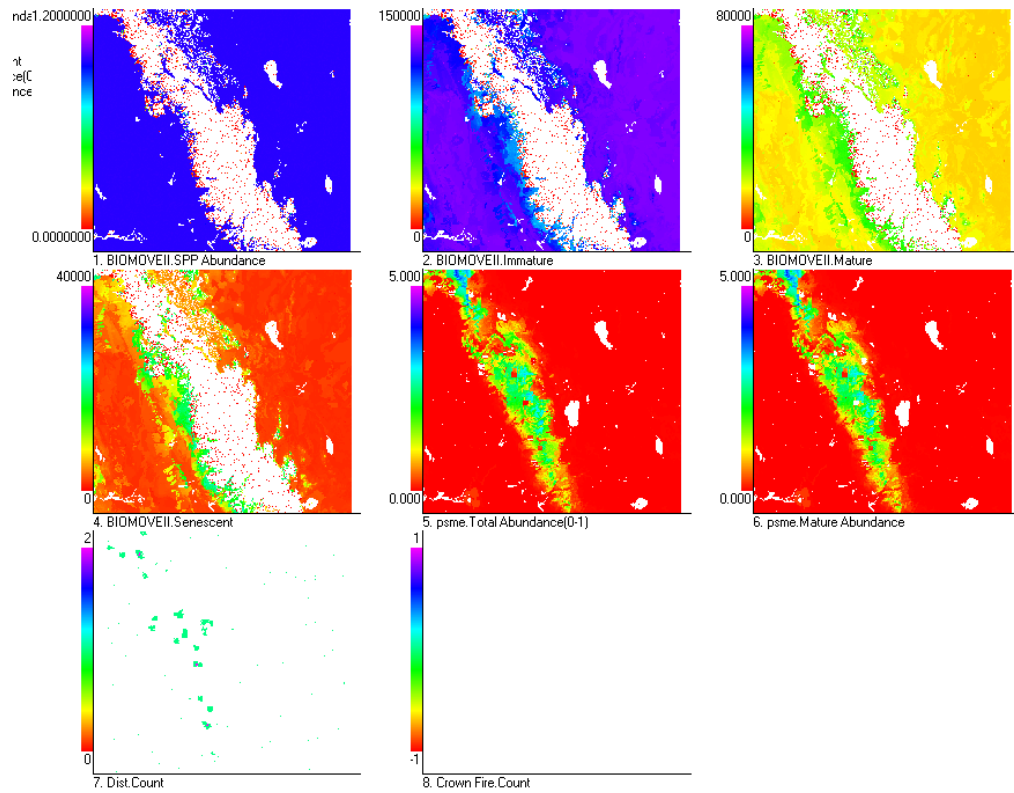
Figure 4.5.5. No crown fires, 0.01% seed long-distance dispersal ability, 10km long-distance dispersal range. Increasing the long-distance dispersal capacity from 4 km to 10 km did not make much difference in the capacity of red brome (denoted "BioMoveII") to disperse potential colonies throughout the study region. This may be due to the high number of individuals of red brome in the regions that are environmentally suitable.
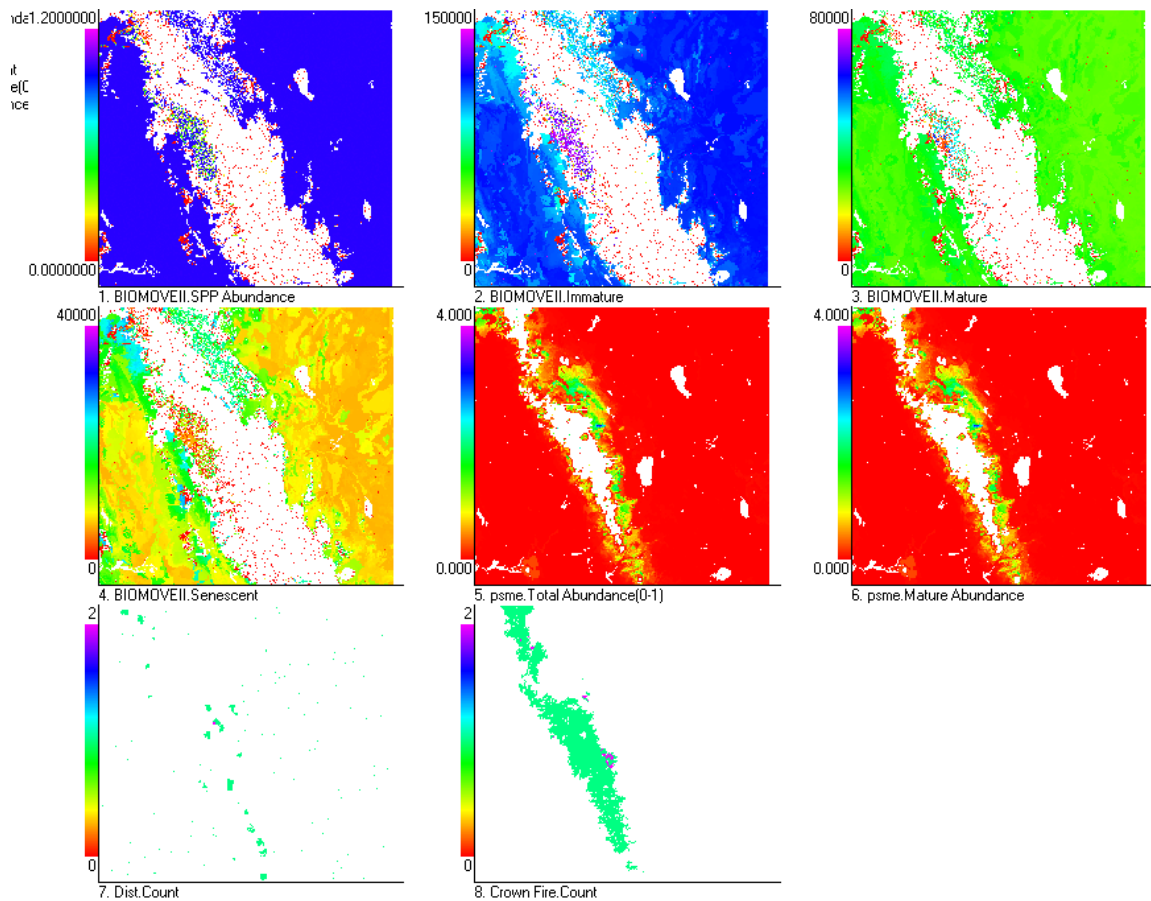
Figure 4.5.6. Most invasive scenario. Crown fires are seen in bottom center, and the effects of the environmental envelope on red brome (denoted "BioMoveII") are minimized, and there were frequent long-distance dispersal events. In this scenario, crown fires were permitted to burn large portions of the mixed conifer zone, as seen in the white sections of the plant functional type ("psme") squares (center and right middle row). This lead to more open areas, in which red brome could establish, seen in the first four boxes as the new bluish polygon along the left (west flank Sierra) side of the white region. In contrast to the previous scenarios, this scenario shows major ecosystem type conversion to grasses for those areas.

4.5.5. Future Research

BioMove scenarios were able to explore several hypotheses about whether mixed coniferous forests will be vulnerable to invasion by *B. madritensis*. The model showed that if the grass is not restricted by its climate envelope — an open question, whether the grass is currently found at lower elevations due to environmental restrictions, competition for light from trees, or some combination — it can at least place propagules throughout the mixed coniferous zone.

Red brome produces dense populations with a potentially high seed production. Under appropriate establishment conditions, it appears that parts of the mixed coniferous forest belt would be affected. However, the largest amount of establishment in the zone was observed when the mixed conifer belt was also experiencing crown fires across the

majority of the region. Under this scenario, the grass was able to show the broadest distribution.

The results suggest altitudinal planting experiments with invasive bromes would help determine whether these species (*B. madritensis and B. tectorum*) are actually limited by climate envelopes at the current time or not.

This version of BioMove is suitable for setting landscape scale ecological questions in a spatially explicit framework. However, the model format should be considered a prototype, with considerably more model sensitivity testing needed. In addition, the stage-based life history matrix had to be adapted to handle the dynamics of invasive annuals. Perhaps different modules could be developed that could be better attuned to the great range of survival strategies exhibited by different plant species. This scenario tested a rather extreme example, by modeling long-lived trees in competition with an invasive annual grass.

A promising area of BioMove is the potential capacity to model the interaction between plant competition and disturbance, in which the competitive advantage switches from one plant to another as a result of disturbance and changing baseline environmental conditions. This scenario showed the capacity for BioMove to simulate such an interaction, and to identify the outer bounds of the dynamics involved. Further research could lead to much better understanding of what landscape patterns would be expected under the differently weighted parameter values.

5.0 Statewide Species Distribution Models

Species distribution models (SDMs) of the ranges of over 300 plant species under current and future climate scenarios were developed by the project as a necessary input to the BioMove simulations. These SDMs are a major modeling resource for assessments of climate change impacts on species in California in their own right. Appendix A lists the species modeled. An example of the output for each species is illustrated in Figure 5.0.1.
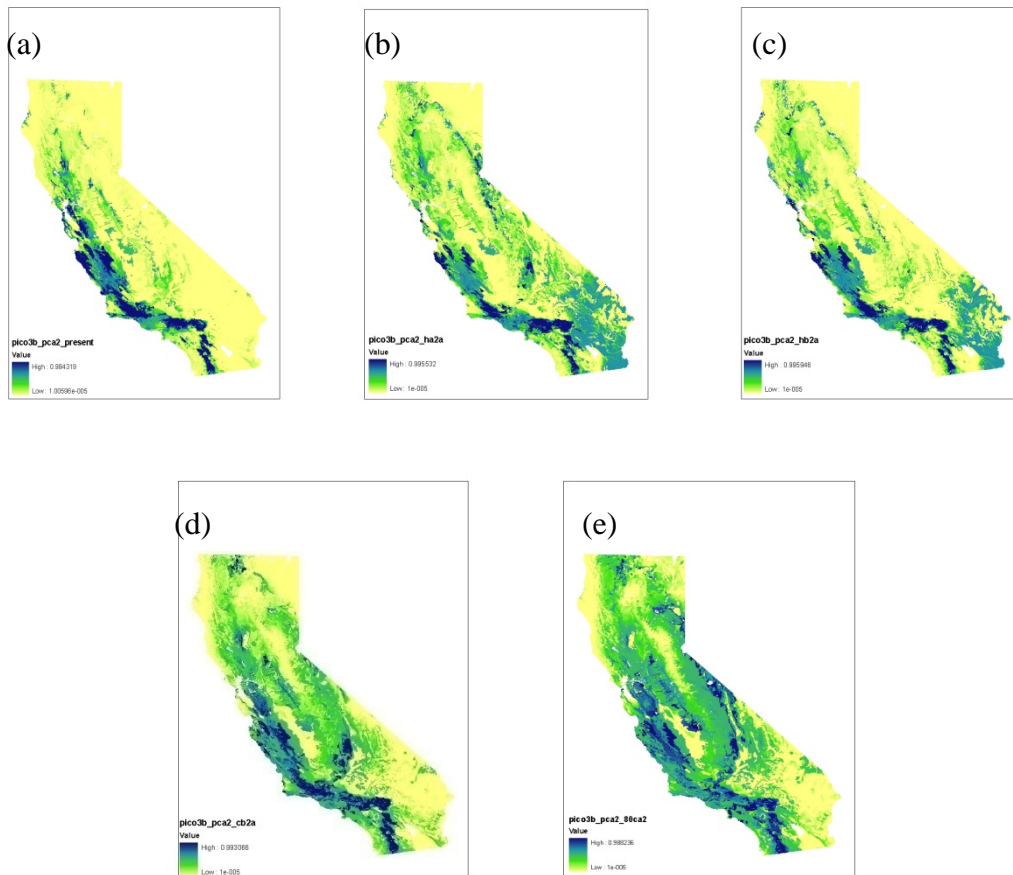
Figure 5.0.1. Example output from species distribution modeling for *Pinus coulterii*. For each species, a present range was predicted using compiled point data (a). Future range predictions were also created for two GCMs; Hadley (b and c) and Canadian (d and e) and two emissions scenarios, A2 (b and d) and B2 (c and e), for 2080. Outputs also were produced for 2050 although not pictured here.

After modeled outputs were created for present, 2050 and 2080, projected changes in species range loss and gain were generated for a group of sample species. First, a cutoff was applied to determine to which probabilities correspond to a species' "presence" and which corresponded to a species' "absence." Presence was assigned a 1 and absence a 0. The present distribution was then subtracted from the future distribution resulting in each cell having a -1 (loss in habitat suitability), 0 (no change in habitat suitability) or 1 (gain in habitat suitability; e.g. Figure 5.0.2).
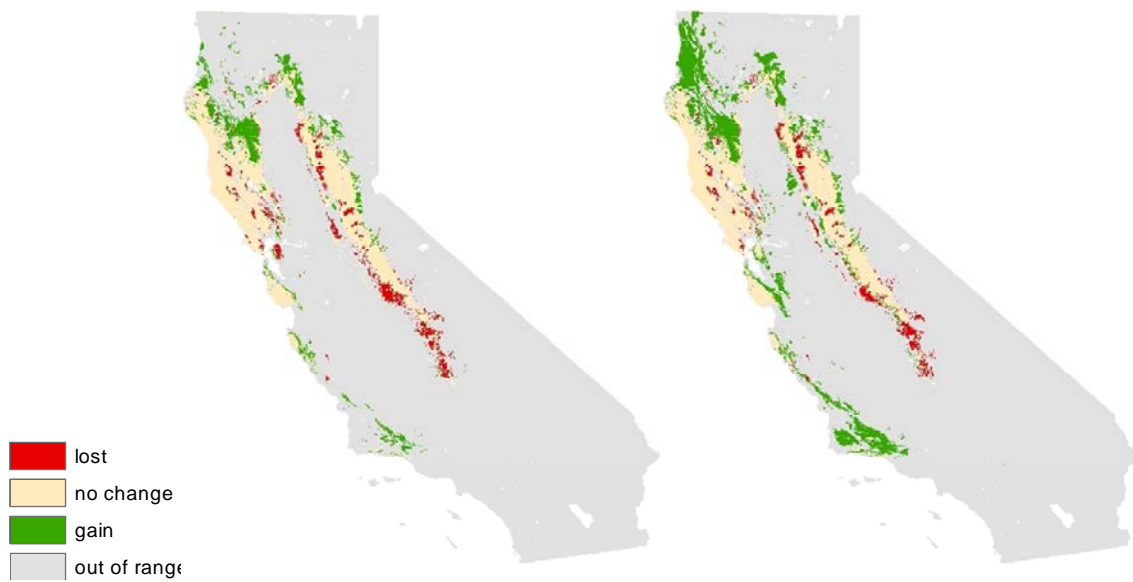
Figure 5.0.2. Projected change in habitat suitability from current to 2080 for example species *Torreya californica* for two scenarios; and Canadian B2 (left) and Canadian A2 (right). Major losses in both scenarios are occurring at the southern edge of the range in the Sierra Nevada. Mountains. Habitat suitability is increasing at the leading edge in the northern Sierra Nevada and Coastal Range for both scenarios with more prominent increases in the Transverse Range predicted under the B2 scenario.

Development of the SDMs required assembly of species presences and absence data. Both presence *and* absence data were because of the range of modeling techniques used, some of which required absence data. Therefore, the traditional source of specimen records was not sufficient for the SDM modeling task. In addition, the majority of herbarium specimens in California have not yet been geo-referenced, so the actual data available from herbaria was relatively low.

Using the presence and absence data, vegetation plots were then assembled. Vegetation plots are useful because, at least for easily identified species, an absence of record at a plot may be assumed to be a real absence. Generous contributions from a variety of groups permitted the assembly of 36,561 vegetation plots (Table 5.0.1), derived from U.S. National Parks, U.S. Forest Service, California Dept. of Fish and Game, U.S. Geological Survey Biological Resources Division, and scientific researchers. Presence only records were then added to this collection, totaling 4,197 for a variety of species that were accessed from digital herbaria repositories at the Jepson Herbarium (UC Berkeley), UC Davis, and Chico State. All georeferenced records used have an original spatial precision within 50m, with the exception of the 1930 Wieslander Vegetation Type Map data, which have spatial precision of +/- 300m (Kelly et al. 2005). All vegetation plot datums and projections were standardized to commonly used California standards: Albers Equal Area projection and North American Datum 1983.

The 40,758 total locations with information about plant species' presence (Figure 5.0.3) were then processed to be used as response variables in the SDM. Processing required

several steps: 1) evaluation of which locality data were suitable to use for modeling which species; 2) development of a list of species to be modeled; 3) preparation of locality data for each species and re-sampling of presence and absence of each species to our base scale for modeling in the state (1km^2); and 4) development of predictor variables for the same localities.
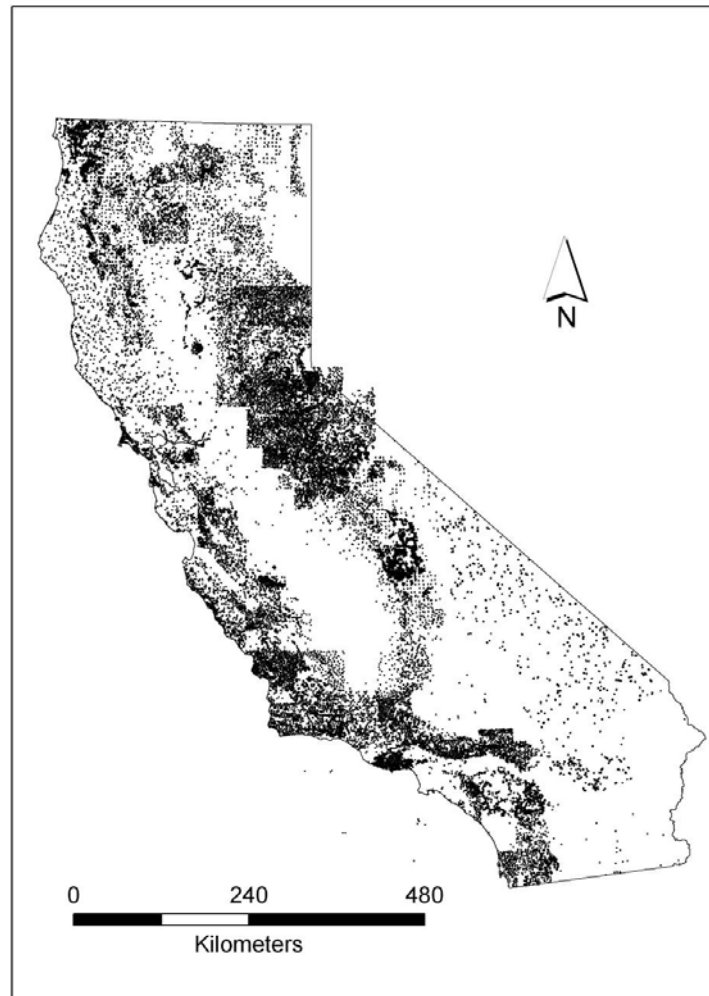
Figure 5.0.3. Locations of plant presence and absence data, used as response variables for species distribution modeling in California.

Source: Data derived from sources listed in Table 5.0.2, this report.

1) To be suitable for modeling, a plant species had to have a minimum of 20 presence records in the collection, resulting in a list of 671 species that were suitable to model. trees, invasive species and certain shrubs were modeled with greatest confidence.

2) This led to a total of 315 species selected for modeling. These species were classified into endemic or non-endemic, and tree, shrub, perennial, annual, or invasive.

3) Once the presence and absence localities for each species were established, the data were resampled to a 1 km x 1 km grid scale for California, resulting in 410,000 grid cells for the state. If any record in a cell indicated a presence of a species, that cell was termed present for that species. Similarly, for absence, if the vegetation plots in a cell did not contain a species' presence, the grid cell was termed absent for that species. Not all P/A records were used for all species sampled- if certain vegetation plots were deemed to not have been surveyed in a manner that would permit identification of certain groups, particularly annual plants, then those sets of plots were excluded from processing for annuals. This was the case, for example with the U.S. Forest Service FIA plots, which were not used for annual species processing. Table 5.0.2 indicates which data sets were used for which species.

4) Development of predictor variables. Predictor variables were developed at a 1 km^2 grid scale. Not all absences were used in determining response variables for the SDMs. The literature suggests that a 2:1 ratio of absence to presence is an appropriate level of absences to avoid model overfit. The number of presences for each species was doubled to identify the number of absences to use. Absences were sampled at random from the total collection of absences identified for each species.

Soil and Climate Predictor Variable Assembly

WorldClim (Hijmans et al. 2005) datasets for predictor climate variables for current climate were used, selecting six of 19 grids available by running a principal components analysis on them over the 410,000 cells of California. This permitted selection of vectors that represented the breadth of California environment, that were biologically important, and that were minimally cross-correlated. The six predictor variables selected were: annual temperature range (Bio 7), mean temperature of the driest quarter (Bio 9), mean temperature of the coldest quarter (Bio 11), precipitation seasonality (Bio 15), precipitation in the wettest quarter (Bio 16), and precipitation of the warmest quarter (Bio 18). WorldClim data are available in 1 km^2 cells. These were used as the geographic framework into which the plot data, as discussed above, was sampled.

Future climatology data were derived from the Hadley Center A2 and B2 scenarios, and the Canadian A2 and B2 scenarios. From these scenario outputs, the same predictor variables were derived as described in the current scenario above. Model outputs were re-sampled to the 1 km^2 framework such that both current and future climate values were available for every cell.

Table 5.0.2. Source of vegetation plots and records used for SDM development.

Dataset	Number of plots used	Used for Pres/Abs (PA) or Pres Only (PO)
American River Survey	338	PO
Central Coast BLM	565	PO
US Forest Service FIA	5517	PO
Serpentine Soils Survey	218	PA
Hastings reserve veg plots (stromberg and griffin)	80	PA
Joshua Tree National Park	300	PA and PO (Rel & RAP)
Los Padres National Forest (Ecoplots)	1299	PA
Sacramento River Plots	92	PA
Mojave Desert Survey (USGS)	1242	PA
PoreCVIS (Point Reyes and GoGa RA)	366	PA
Redwoods National Park	194	PO
Santa Monica Mtns. NRA	2875	PA
Sequoia National Park (CVIS)	627	PA
Sequoia National Park (RAP)	123	PO
Sequoia National Park VM AA	2821	PO
Sequoia National Park VMPlots	423	PO
Cal Dept Fish & Game Sierra Foothills RAP	648	PO
Cal Dept Fish & GameSierra Foothills Relevees	296	PA
Sudden Oak Death Surveys	98	PO
Suisun Marsh	67	PO
USFS No Cal Ecoplots ("USFSN")	5643	PA
USFS So Cal Ecoplots ("White Data")	906	PO
Wieslander Vegetation Type Maps	10860	PO
Western Riverside (USGS)	368	PO
Yosemite National Park	595	PO
Total plots available	36561	
Herbarium records	4197	PO
Total Data	40758	

The State Soil Geographic Data Base (STATSGO), which is appropriate for regional-scale research, was developed by the USDA-NRCS. The mapping scale for STATSGO map is 1:250000. STATSGO delineates soil map units comprised of similar combinations of soil components or series as a GIS layer. In addition, the STATSGO database contains soil characteristics data on many physical, chemical, and biological attributes of each

component and layer (or horizon), including their proportional fraction of the map units. Each characteristic is described as a range, with a low and high value. EPA aggregated the layer and component soil characteristics to map unit soil characteristics for 27 variables related to water quality (Shirazi et al. 2001).

EPA provided a table of the map unit-level characteristics for the study area. This table was joined to the STATSGO GIS layer of map units and converted to a grid of soil characteristics at the same 1 km^2 resolution as the climate and species plot data. Of the 27 characteristics in the EPA table, five that could strongly influence plant species distribution in California were selected for this project, using the low value of the range for each. The five soil characteristic variables were: Available water capacity (cm cm^{-1}), soil depth (m), pH, salinity (mmhos cm^{-1}), and depth to water table (m).

A probabilistic model based on Bayesian decision rules was used to examine the impact of including static environmental predictor variables such as soils maps in combination with dynamic variables such as climate on the identification of potential range and a consensus model based on PCA to reduce the uncertainty of predictive range mapping using a variety of individual model outputs. The AUC statistics were calculated to evaluate the effects of model. The AUC was recorded for each model run of each species.

5.1.1. Species Distribution Models

Species presences and absences and predictor environmental values were compiled for each grid cell, and extracted to tabular form. Once the data were in tabular format, they were exported to R (R Development Core Team 2006), where five SDMs (General Boosted Regression (GBM), Classification and Regression Tree analysis (CART), Artificial Neural Net (ANN), General Additive Model (GAM), and General Linear Model (GLM) were run using BioMod, a modeling framework developed for use in R (Thuiller 2003). SDM model outputs from R were stored in tabular format (.dbf). A principal components analysis was conducted on the model outputs to derive a single, best estimate output for each climate scenario. The final model outputs were converted to floating point grid files and made available for use as inputs to BioMove.

5.1.2. Data Archive

The data from these species distribution models will be made available through archiving. The data will be housed in a permanent archive at the National Center for Ecological Analysis and Synthesis (NCEAS) at UCSB. This archive will be available to many ecological and conservation working groups interested in climate change at NCEAS, making this data a valuable resource for researchers from around the world interested in data useful for testing climate change theory. The same archive will be freely available to California researchers as well. The Nature Conservancy will maintain a copy of the data in their San Francisco offices, so collaborators in their program may find it more convenient to access that data set. Public enquiries will be entertained at the NCEAS archive, however. Finally, Conservation International is developing a data portal website for its Center for Applied Biodiversity Sciences (CABS). As soon as that portal is operational, the data will be made available through that venue as well. All

data at NCEAS and CABS will be associated with full metadata, following NCEAS protocols.

6.0 Conclusions and Recommendations

BioMove is a hybrid model uniquely suited to modeling species range shifts in response to climate change. Its hybrid nature is facilitated by implementation in the Landscape Modeling Shell, Lamos. Elements simulating dispersal, disturbance and competition are available for interface with BioMove, while BioMove itself simulates population dynamics and succession. The model is therefore a versatile tool, applicable to many of California's unique biogeographic settings.

Tests of BioMove indicate that it is useful for examination of the influences of fire, life history and land use on species' response to climate change. Species' range shifts across land ownership mosaics have been tested, as has the spread of invasive species and the effect of fire on the response of trees and grasses to climate change. Assessments of flagship species such as the Joshua tree have been demonstrated with BioMove. Many other applications are anticipated as the tool is distributed to the research community.

An important input to BioMove is species distribution models, which have been developed for over 300 species from a database of over 25,000 vegetation plots statewide. Each species has been modeled using 6 distribution models for each of eight climate scenarios, making for 48 scenarios available for each species. This modeling archive is in itself a remarkable resource for climate change and biodiversity impact studies in California. It will be archived at the National Center for Ecological Analysis and Synthesis and updated periodically.

Among the future uses of BioMove are assessments of species extinction risk from climate change, examination of policy questions and examination of fire dynamics. Members of the BioMove development team are helping design tools for international red-list designation of threatened species. Applications in state and federal endangered species programs are foreseen. Policy questions can be addressed using BioMove, such as the biological impact of overshoot of greenhouse gas stabilization targets and return to lower levels. Fire dynamics in California forest and shrub communities as climate changes can be productively explored. Many problems with unique dynamic elements, including land use change problems, will be amenable to assessment with the model.

BioMove is especially relevant for interface with novel fine-scale climatologies for site assessment. The model is scale independent, meaning that it can be implemented at any scale. Applications at 10m-30m are within the capability of BioMove and supported by environmental information layers such as digital elevation models. The limiting factor to date in these fine-scale applications has been the availability of future climate scenarios, since global and regional climate models typically operate on scales of hundreds and tens of kilometers respectively, three orders of magnitude coarser than the fine scale grains at which many biological processes might suitably be simulated.

NCEAS, the Bren School of Environmental Science, and the Nature Conservancy are collaborating on a working group to develop methods for creating fine-scale climate scenarios for site assessment that will be implementable in BioMove. The first of these

meetings will be held in September 2008. By combining lines of evidence and global and fine-scale modeling, this group hopes to produce a groundbreaking method for producing climatologies with resolutions of tens of meters. BioMove will stand well situated to take advantage of these climatologies for site assessment.

Understanding of fire ecology in a changing climate is another research frontier in which BioMove can feature prominently. The interchangeable fire module in BioMove implementation makes the model a flexible fire simulation tool on broad-to-meso scales (and with suitable climatologies, on site scales as well). More sophisticated implementation of BioMove in support of fire climate change ecology studies is a major research goal for the development team.

Beyond its free availability, BioMove will be promoted in the international research community through publications, presentations and management applications. Test versions of the model have already been requested by researchers around the world with no advance publicity other than word of mouth, and the model has been used in applications ranging from the San Diego 2050 assessment to air pollution and conservation planning assessments in the south coast and Sierra foothills. Upcoming publication of the model methods in a major peer-review modeling journal will feature online access and a user's manual.

Advanced applications of the model will be promoted by the C4 collaboration, a joint initiative of NCEAS, the Nature Conservancy, Conservation International, the Wildlife Conservation Society and local conservation groups such as the Greater Yellowstone Coalition and Fanamby (Madagascar). BioMove will be available for all C4 working groups at NCEAS, in combination with species data sets and advanced fine-scale climate projections with which to run the model. These applications will provide high-profile publications using BioMove as well as facilitating its application in local climate change management exercises — the purpose of C4 is to link local applications with world-class appropriate science — and BioMove is a tailored to meet both of these needs.

Finally, because BioMove will be widely available, many researchers will be able to experiment with its capabilities and develop new applications. Site-scale modeling, explorations of fire-vegetation interactions, and facilitating the interface of world-class science and local impact assessment are but a few of its potential applications. Other applications can be expected that have not been anticipated in the development or testing process. BioMove will undoubtedly move the field ahead to more advanced questions, which more sophisticated models and more advanced versions of BioMove will be required to address. The speed and complexity of those advances will be one measure of the contributions of BioMove.

7.0 References

Allen-Diaz, B. H. and J. W. Bartolome. 1992. "Survival of *Quercus douglasii* (Fagaceae) seedlings under the influence of fire and grazing." *Madroño* 39:47-53.

Bartolome, J. W., M. P. McClaran, B. H. Allen-Diaz, J. Dunne, L. D. Ford, R. B. Standiford, N. K. McDougland and L. C. Forero. 2001. Effects of fire and browsing on regeneration of blue oak in R. B. Standiford, M. D., and K. L. Purcell, editors. "Proceedings of the Fifth Symposium on Oak Woodland: Oaks in California's Changing Landscape." Pacific Southwest Research Station, Forest Service, U.S. Department of Agriculture, San Diego, CA.

Beatley, J.C. 1966. "Ecological status of introduced grasses (*Bromus* spp.) in desert vegetation of Southern Nevada." *Ecology* 47:548-554.

Beckstead, J., S.E. Meyer, C.J. Molder and C. Smith. 2007. "A race for survival: Can *Bromus tectorum* seeds escape *Pyrenophora semeniperda*-caused mortality by germinating quickly?" *Annals of Botany* 99:907-914

Bloomgarden, C. A. 1995. "Protecting endangered species under future climate change: From single-species preservation to an anticipatory policy approach." *Environmental Management* 19:641-648.

Bolsinger, C. L. 1988. "The hardwoods of California's timberlands, woodlands, and savannas." *Resource Bulletin PNW-RB-GTR-160*. Albany (CA): Pacific Southwest Research Station, Forest Service, U.S. Department of Agriculture: 1-30.

Borchert, M. I., F. W. Davis, J. Michaelsen and L. D. Oyler. 1989. "Interactions of factors affecting seedling recruitment of blue oak (*Quercus douglasii*) in California." *Ecology* 70:389-404.

Botkin D.B., H. Saxe, M.B. Araujo, et al. 2007. « Forecasting the effects of global warming on biodiversity." *Bioscience* 57 (3): 227-236.

Brooks, M. and K. Berry. 1999. "Ecology and management of alien annual plants in the California deserts." *CalEPPC News* (California Exotic Pest Plant Council Newsletter) 7: 4-6.

Brooks M.L., C.M. D'Antonio, D.M. Richardson, J.B. Grace, J.E. Keeley, et al. 2004. "Effects of invasive alien plants on fire regimes." *BioScience* 54:677–688.

Brooks M.L. and T.C. Esque. 2002. "Alien annual plants and wildfire in desert tortoise habitat: Status, ecological effects, and management." *Chelonian Conservation and Biology* 4:330–340.

Brown, T. J., B. L. Hall, and A. L. Westerling. 2004. "The impact of twenty-first century climate change on wildland fire danger in the western United States: An applications perspective." *Climatic Change* 62:365-388.

Bush, M. B., M. R. Silman, and D. H. Urrego. 2004. "48,000 years of climate and forest change in a biodiversity hot spot." *Science* 303:827-829.

Clark, J. S. 1998. "Why trees migrate so fast: Confronting theory with dispersal biology and the paleorecord." *American Naturalist* 152:204-224.

Clark, J. S., C. Fastie, G. Hurtt, S. T. Jackson, C. Johnson, G. A. King, M. Lewis, J. Lynch, S. Pacala, C. Prentice, E. W. Schupp, T. Webb, III, and P. Wyckoff. 1998. "Reid's paradox of rapid plant migration — Dispersal theory and interpretation of paleoecological records." *BioScience* 48:13-24.

Commission, I. S. S. 2001. *IUCN Red List Categories and Criteria : Version 3.1*. IUCN, Gland, Switzerland and Cambridge, UK (2001). IUCN, Gland, Switzerland and Cambridge, UK.

Coope, G.R. 1995. "Insect faunas in iceage environments: why so little extinction?" In *Extinction Rates*. Eds. John H. Lawton, Robert M. May. Oxford University Press, Oxford. pp. 55-74.

Davis, A. J., L. S. Jenkinson, J. H. Lawton, B. Shorrocks, and S. Wood. 1998. "Making mistakes when predicting shifts in species range in response to global warming." *Nature London* 391:783-786.

Davis, F. W., D. M. Stoms, A. D. Hollander, K. A. Thomas, P. A. Stine, D. Odion, M. I. Borchert, J. H. Thorne, M. V. Gray, R. E. Walker, K. Warner, and J. Graae. 1998. *The California gap analysis project.* Final Report. University of California, Santa Barbara.

Davis, M. B. 1994. "Ecology and paleoecology begin to merge." *Trends in Ecology and Evolution* 9:357-358.

Dole, K.P., M.E. Loik, and L.C. Sloan. 2003."The relative importance of climate change and the physiological effects of CO_2 on freezing tolerance for the future distribution of *Yucca brevifolia*." *Global and Planetary Change* 36: 137-146.

Emming, J. 2005. "Special conservation report: Nevadagascar? The threat that invasive weeds and wildfires pose to our North American desert biomes. Part 1: The Mojave Desert and Joshua tree woodlands." *Cactus and Succulent Journal* 77: 302-312.

Ficetola, G. F., W. Thuiller, and C. Miaud. 2007. "Prediction and validation of the potential global distribution of a problematic alien invasive species — the American bullfrog." *Diversity and Distributions* 13:476-485.

Flenley, J. R. 1998. "Tropical forests under the climates of the last 30,000 years." *Climatic Change* 39:177-197.

Fowells, H. A. and G. H. Schubert. 1965. "Sugar pine (*Pinus lambertiana* Dougl.)." In *Silvics of forest trees of the United States*. p. 464-470. U.S. Department of Agriculture, *Agriculture Handbook 271*. Washington, DC.

Gear A.J. and B. Huntley B. 1991. "Rapid changes in the range limits of Scots Pine 4,000 years ago." *Science* 251:544–547.

Graham, R. W. and E. C. Grimm. 1990. "Effects of Global Climate Change on the Patterns of Terrestrial Biological Communities." *Trends in Ecology and Evolution* 5:289-292.

Gorder, J., R. Shaw and R. Whitney. 2005. *Joshua Tree National Park: Fire management plan. Environmental Assessment*. Twentynine Palms, CA: U.S. Department of the Interior, National Park Service, Joshua Tree National Park (Producer). http://www.nps.gov/jotr/parkmgmt/upload/fire.pdf

Grinnell, K. 1917. "The niche-relationships of the California thrasher." *The Auk* 34(4): 427-433.

Guo, Q.F. 2004. "Slow recovery in desert perennial vegetation following human disturbance." *Journal of Vegetation Science* 15: 757-762.

L. Hannah, G. F Midgley, T Lovejoy, W. J Bond, M Bush, J. C Lovett, D Scott, and F. I Woodward. 2002. "Conservation of Biodiversity in a Changing Climate." *Conservation Biology* 16 (1): 264–268

Harte, J., A. Ostling, J. L. Green, and A. Kinzig. 2004. "Climate Change and Extinction." *Nature* (online).

Hayhoe K, D. Cayan, C.B., Field, et al. 2004. "Emissions pathways, climate change, and impacts on California." *Proceedings of the National Academy of Sciences of the United States of America* 101(34):12422-12427.

Heikkinen R.K., M. Luoto, A.B. Araujo, et al. 2006. "Methods and uncertainties in bioclimatic envelope modeling under climate change." *Progress in Physical Geography* 30 (6): 751-777.

Hickman, J.C.E. 1993. *The Jepson manual: higher plants of California*. University of California Press, Berkeley, CA.

Higgins, S.I., R. Nathan and M.L.Cain. 2003. "Are long-distance dispersal events in plants usually caused by nonstandard means of dispersal." *Ecology* 84:1945–1956.

Hijmans, R. J., S. E. Cameron, J. L. Parra, P. G. Jones, and A. Jarvis. 2005. "Very high resolution interpolated climate surfaces for global land areas." *International Journal of Climatology* 25: 1965-1978.

Houghton, J.T., Y. Ding, D.J. Griggs, M. Noguer, P.J. van der Linden, X. Dai, K. Maskell, C.A. Johnson. 2001. *Climate Change 2001: The Scientific Basis. Contributions of*

Working Group 1 to the Third Assessment Report of the Intergovernmental Panel on Climate Change. Cambridge University Press, Cambridge.

O. Hoegh-Guldberg, P. J. Mumby, A. J. Hooten, R. S. Steneck, P. Greenfield, E. Gomez, C. D. Harvell, P. F. Sale, A. J. Edwards, K. Caldeira, N. Knowlton, C. M. Eakin, R. Iglesias-Prieto, N. Muthiga, R. H. Bradbury, A. Dubi, M. E. Hatziolos. 2007. "Coral Reefs Under Rapid Climate Change and Ocean Acidification." *Science* 318 (5857): 1737 - 1742

Hunter, R. 1991. "*Bromus* invasions on the Nevada Test Site: present status of *B. rubens* and *B. tectorum* with notes on their relationship to disturbance and altitude." *Great Basin Naturalist* 51:176-182.

Huntingford, C., and J. Lowe. 2007. "'Overshoot' scenarios and climate change." *Science* 316:829-829.

Kinzig, A. P., and J. Harte. 2000. "Implications of endemics-area relationships for estimates of species extinctions." *Ecology* 81:3305-3311.

Huntley, B. 1991. "How Plants Respond to Climate Change: Migration Rates, Individualism and the Consequences for Plant Communities." *Annals of Botany* 67: 15-22, 1991.

Huntley, B., T. Webb III., eds. 1998. *Vegetation history*. Dordrecht ; Boston : Kluwer Academic Publishers.

Hutchinson, G. E. 1957. "Concluding remarks, Cold Spring Harbor Symposium." *Quaternary Biology* 22:415-427.

Huxman, T.E., H. Hamerlynck, S.D Smith. 1999. "Reproductive allocation and seed production in *Bromus madritensis* ssp. *rubens* at elevated atmospheric CO_2." *Functional Ecology* 13:769-777.

Keeley J. E. 2005. "Fire management impacts on invasive plants in the western United States." *Conservation Biology* 20:375-384.

Kelly M., B. Allen-Diaz, and N. Kobzina. 2005. "Digitization of a historic dataset: the Wieslander California Vegetation Type Mapping Project." *Madroño* 52:191-201.

Kinloch, B.B. and W.H. Scheuner. 1990. "Silvics of North America: 1. Conifers; 2. Hardwoods." *Agriculture Handbook 654*. U.S. Department of Agriculture, Forest Service, Washington, D.C. vol.2, 877 p.

Kinzig, A. P. and J. Harte. 2000. "Implications of endemics-area relationships for estimates of species extinctions." *Ecology* 81:3305-3311.

Krugman, S. L. and J.L. Jenkinson. 1974. "*Pinus L.* Pine." In *Seeds of woody plants of the United States*. p. 598-638. C. S. Schopmeyer, tech. coord. U.S. Department of Agriculture, Agriculture Handbook 450. Washington, DC.

Lenz, L. W. 2001. "Seed dispersal in *Yucca brevifolia* (Agavaceae) —present and past, with consideration of the future of the species." *Aliso* 20: 61-74.

Loiselle, B. A., C. A. Howell, C. H. Graham, J. M. Goerck, T. Brooks, K. G. Smith, and P. H. Williams. 2003. "Avoiding pitfalls of using species distribution models in conservation planning." *Conservation Biology* 17:1591-1600.

Lovejoy, T. E., and L. Hannah. 2005. "Global Greenhouse Gas Levels and the Future of Biodiversity." In T. E. Lovejoy, and L. Hannah, editors. *Climate Change and Biodiversity*. Yale University Press, New Haven.

Mack R.N. and D.A. Pyke. 1983. "The demography of *Bromus tectorum*: Variation in Time and Space." *The Journal of Ecology* 71:69-93.

Malcolm, J. R., C. Liu, R. P. Neilson, L. A. Hansen, and L. Hannah. 2006. "Global Warming and Extinctions of Endemic Species from Biodiversity Hotspots." *Conservation Biology* 20(2): 538-548.

Markham, A. 1996. "Potential impacts of climate change on ecosystems: A review of implications for policymakers and conservation biologists." *Climate Research* 6:179-191.

McClaran, M. P. 1983. Quercus douglasii *stand age structure on grazed and ungrazed sites in Tulare County, California*. 17 p. Report to the Sequoia Natural History Association; Three Rivers, California. Department of Forestry and Resource Management, University of California, Berkeley 94720.

Moore, A.D and I.R. Noble. 1990. "An individualistic model of vegetation stand dynamics." *Journal of Environmental Management* 31(1):61-81.

Norton, J.B., T.A. Monaco, and U. Norton. 2007. "Mediterranean annual grasses in western North America: kids in a candy store." *Plant Soil* 298:1-5.

O'Neill, B. C. and M. Oppenheimer. 2002. "Climate Change: Dangerous Climate Impacts and the Kyoto Protocol." *Science* 296:1971-1972.

Overpeck, J.T., C. Whitlock, and B. Huntley. 2003. "Terrestrial biosphere dynamics in the climate system: past and future." In: *Paleoclimate, global change and the future* (IGBP Synthesis Volume), K. Alverson, R. Bradley, and T. Pedersen, eds., Springer-Verglag, Berlin, pp. 81-111.

Parker-Allie, F., C. F. Musil, and W. Thuiller. 2007. "Effects of climate warming on the distributions of invasive European annual grasses: A southern African perspective." *South African Journal of Botany* 73:306-306.

Parmesan C., N. Ryrholm, C. Stefanescu, et al. 1999. "Poleward shifts in geographical ranges of butterfly species associated with regional warming." *Nature* 399(6736): 579-583.

Parmesan, C. and G. Yohe. 2003. "A globally coherent fingerprint of climate change impacts across natural systems." *Nature* 421:37-42.

Pavlik, B.M., P.C. Muick, S.G. Johnson and M. Popper. 1991. *Oaks of California*. Cachuma Press. Los Olivos, California.

Pearson, R. G. 2006. "Climate change and the migration capacity of species." *Trends in Ecology & Evolution* 21:111-113.

Pearson, R. G. and T. P. Dawson. 2005. "Long-distance plant dispersal and habitat fragmentation: identifying conservation targets for spatial landscape planning under climate change." *Biological Conservation* 123:389-401.

Peterson, A. T., M. A. Ortega-Huerta, J. Bartley, V. Sanchez-Cordero, J. Soberon, R. H. Buddemeier, and D. R. Stockwell. 2002. "Future projections for Mexican faunas under global climate change scenarios." *Nature* 416:626-629.

Pierson, E. A. and R.N. Mack. 1990. "The population biology of *Bromus tectorum* in forests: distinguishing the opportunity for dispersal from environmental restriction." *Oecologia* 84:519-525.

R Development Core Team. 2006. *R: A language and environment for statistical computing*. R Foundation for Statistical Computing, Vienna, Austria.

Rice, K. J. and Mack, R. N. 1991. "Ecological genetics of *Bromus tectorum*." *Oecologia* 88:91-101.

Richardson, D. M., and W. Thuiller. 2007. "Home away from home — objective mapping of high-risk source areas for plant introductions." *Diversity and Distributions* 13:299-312.

Ritter, L. V. 1998. "Blue oak woodland." Page 4. *California Wildlife Habitat Relationships System*. California Department of Fish and Game, California Interagency Wildlife Task Group.

Root, T.L., J.T. Price, K.R. Hall, S.H. Schneider, C. Rosenzweig, and J. A. Pounds. 2003. "Fingerprints of global warming on wild animals and plants." *Nature* 421:57–60.

Salo, L.F. 2004. "Population dynamics of red brome (*Bromus madritensis* subsp. Rubens): times for concern, opportunities for management." *Journal of Arid Environments* 57:291-296.

Salo, L.F. 2005. "Red brome (*Bromus madritensis*) in North America: possible modes for early introductions, subsequent spread." *Biological Invasions* 7:165-180.

Shirazi, M. A., L. Boersma, P. K. Haggerty and C. B. Johnson. 2001. "Spatial extrapolation of soil characteristics using whole-soil particle size distributions." *Journal of Environmental Quality* 30(1):101-111.

Smith, B., I.C. Prentice, and M.T. Sykes. 2001. "Representation of vegetation dynamics in the modeling of terrestrial ecosystems: comparing two contrasting approaches within European climate space." *Global Ecology and Biogeography* 10 (6):621–637.

Smith, S.D., T.L. Hartstock, and P.S. Nobel. 1983. "Ecophysiology of *Yucca brevifolia*, an arborescent monocot of the Mojave desert." *Oecologia* 60:10-17.

Swiecki, T. J., E. A. Bernhardt, and C. Drake. 1993. *Factors affecting blue oak sapling recruitment and regeneration.* Pages 1-142. Prepared for: Strategic Planning Program, California Department of Forestry and Fire Protection, Contract 8CA17358.

Thomas, C. D., A. Cameron, R. E. Green, M. Bakkenes, L. Beaumont, A. Grainger, Y. Collingham, B. F. Erasmus, M. Ferreira de Siqueira, L. Hannah, L. Hughes, B. Huntley, A. T. Peterson, A. van Jaarsveld, G. F. Midgely, L. Miles, M. Ortega-Huerta, O. Phillips, and S. Williams. 2004. "Extinction risk from climate change." *Nature* 427:145-148.

Thuiller, W. 2003. "BIOMOD — optimizing predictions of species distributions and projecting potential future shifts under global change." *Global Change Biology* 9:1353-1362.

Thuiller, W., C. Albert, M.B. Araujo, et al. 2008. "Predicting global change impacts on plant species' distributions: Future challenges." *Perspectives in Plant Ecology, Evolution and Systematics* 9 (3-4):137-152.

Turner, R. M. 1982. "Mojave dessert scrub." In Brown, D.E. ed. *Biotic communities of the American Southwest —United States and Mexico desert plants.*

Tyler, C.M., F.W. Davis, B. Mahalla. 2008. "The relative importance of factors affecting age-specific seedling survival of two co-occurring oak species in southern California. " *Forest Ecology and Management* 255(7): 3063-3074.

Tyler, C.M., B. Kuhn, and F.W. Davis. 2006. "Demography and recruitment limitations of three oak species in California. "*The Quarterly Review of Biology* 81:127-152.

University of California, SNEP Science Team and Special Consultants. 1996. *People and Resource Use in Status of the Sierra Nevada: Sierra Nevada Ecosystems Project Final Report to Congress*. SNEP Vol 1 Chapter 2. Regents of the University of California.

Van Mantgem, P.J., N.L. Stephenson, and J.E. Keeley. 2004. "Forest reproduction along a climatic gradient in the Sierra Nevada, California. " *Forest Ecology and Management* 225:319-399.

Van Mantgem, P.J. and N.L. Stephenson. 2007. "Apparently climatically induced increase of tree mortality rates in a temperate forest. " *Ecology Letters* 10 (10): 909-916.

Vander Wall, S. B., T. Esque, D. Haines D M. Gernett, B.A. Waitman. 2006. " Joshua tree (*Yucca brevifolia*) seeds are dispersed by seed-caching rodents. " *Ecoscience* 13:539-543.

Walther G., E. Post, P. Convey, A. Menzel, C. Parmesan, T. Beebee, J. Fromentin, O. Hoegh-Guldberg and F. Bairlein. 2002. "Ecological responses to recent climate change. " *Nature* 416: 389-395.

Went, F. W. 1948. "Ecology of desert plants. I. Observations on germination in the Joshua Tress National Monument, California. " *Ecology* 29: 242-253.

Westerling, A. L., A. Gershunov, T. J. Brown, D. R. Cayan, and M. D. Dettinger. 2003. "Climate and wildfire in the western United States. " *Bulletin of the American Meteorological Society* 84:595-623.

Westerling, A. L., H. G. Hidalgo, D. R. Cayan, and T. W. Swetnam. 2006. "Warming and earlier spring increase western US forest wildfire activity. " *Science* 313:940-943.

8.0 Glossary

Acronym	Description
ANN	Artificial Neural Network
AUC	Area Under Curve
BioMOD	Biodiversity Modeling
CART	Classification and Regression Tree
DGVM	Dynamic Global Vegetation Model
EAR	Endemic Area Relationship
GAM	Generalized Additive Model
GBM	General Boosting Model
GCM	General Circulation Model
GUI	Graphical User Interface
IUCN	The International Union for Conservation of Nature
Lamos	Landscape Modeling Shell
PCA	Principal Components Analysis
PFT	Plant Functional Type
RCM	Regional Circulation Model
SAR	Species Area Relationship
SDM	Species Distribution Model
UNFCCC	United Nations Framework Convention on Climate Change

Appendix A

Species modeled with BioMOD and key to species codes in data archive.

The species in this list have been modeled using BioMod in at least four and for most species six different species distribution models (SDM), and a consensus model has been produced which represents the strongest common axes of agreement among the SDMs. Each BioMod output is available for two GCMs, two emissions scenarios each, and for two time periods (2050 and 2080), meaning that for each species listed, up to 44 individual models are available.

SPECIES NAME	Species Code
Abies concolor	ABCO
Abies magnifica	ABMA
Acacia greggii	ACGR
Acamptopappus shockleyi	ACSH
Acamptopappus sphaerocephalus	ACSP
Acer negundo californicum var. californicum	ACNEC2
Achnatherum hymenoides	ACHY
Achnatherum coronatum	ACCO21
Achnatherum speciosum	ACSP12
Adenostoma sparsifolium	ADFA
Adenostoma fasciculatum	ADSP
Aesculus californica	AECA
Allionia incarnata	ALIN
Allium amplectens	ALAM2
Alnus rhombifolia	ALRH2
Alnus incana	ALIN2
Alnus rubra	ALRU2
Amaranthus fimbriatus	AMFI
Ambrosia dumosa	AMDU2
Amelanchier utahensis	AMUT
Amorpha californica var. californica	AMCAC
Arbutus menziesii	ARME
Arctostaphylos canescens	ARCA5
Arctostaphylos glandulosa	ARGL3
Arctostaphylos glauca	ARGL4
Arctostaphylos luciana	ARLU4

Arctostaphylos manzanita	ARMA
Arctostaphylos nevadensis	ARNE
Arctostaphylos patula	ARPA6
Arctostaphylos pungens	ARPU5
Arctostaphylos viscida	ARVI4
Arenaria macradenia	ARMA3
Aretmesia nova	ARNO4
Aristida purpurea	ARPU9
Artemisia californica	ARCA11
Artemisia douglasiana	ARDO3
Artemisia dracunculus	ARDR4
Artemisia ludoviciana	ARLU
Artemisia rothrockii	ARRO4
Artemisia tridentata	ARTR2
Artemisia tridentata vaseyana	ARTRV
Arundo donax	ARDO4
Asclepias erosa	ASER2
Asclepias subulata	ASSU
Aspidotus californica	ASCA5
Astragalus lentiginosus	ASLE8
Atriplex canescens	ATCA2
Atriplex confertifolia	ATCO
Atriplex hymenelytra	ATHY
Baccharis pilularis	BAPI
Baccharis salicifolia	BASA4
Bebbia juncea	BEJU
Berberis aquifolium var. dictyota	BEAQD
Bouteloua barbata	BOBA2
Bouteloua eriopoda	BOER4
Brickellia atractyloides	BRAT
Bromus carinatus	BRCA5
Bromus diandrus	BRDI3
Bromus hordeaceus	BRHO2
Bromus madritensis	BRMA3
Bromus tectorum	BRTE
Calamagrostis breweri	CABR
Calium californicum	GACA3
Calocedrus decurrens	CADE27

Calochortus albus	CAAL2
Calochortus amoenus	CAAM5
Calochortus invenustus	CAIN3
Calochortus splendens	CASP
Calycanthus occidentalis	CAOC5
Castanopsis chrysophylla	CACH6
Castilleja affinis	CAAF
Castilleja affinis subsp affinis	CAAFA2
Castilleja angustifolia	CAAND
Castilleja foliolosa	CAFO2
Castilleja lemmonii	CALE18
Castilleja nana	CANA3
Ceanothus crassifolius	CECR
Ceanothus cuneatus	CECU
Ceanothus cuneatus var. fascicularis	CECUF2
Ceanothus greggii	CEGR
Ceanothus integerrimus	CEIN3
Ceanothus jepsonii	CEJE
Ceanothus leucodermis	CELE2
Ceanothus megacarpus	CEME
Ceanothus oliganthus	CEOL
Ceanothus prostratus	CEPR
Ceanothus spinosus	CESP
Ceanothus tomentosus	CETO
Ceanothus velutinus	CEVE
Centaurea melitensis	CEME2
Centaurea solstitialis	CESO3
Cercis occidentalis	CECAT
Cercis occidentalis var. orbiculata	CEOCO
Cercocarpus betuloides	CEBE3
Cercocarpus ledifolius	CELE3
Chaenactis douglasii	CHDO
Chamaebatia foliolosa	CHFO
Chamaecyparis lawnsoniana	CHLA
Cheilanthes parryi	CHPA4
Cheilanthes viscida	CHVI2
Chorizanthe rigida	CHRI

Chrysolepis sempervirens	CHSE11
Chrysothamnus viscidiflorus	CHVI8
Cirsium occidentale	CIOC
Cirsium occidentale var. venustum	CIOCV
Coreopsis bigelovii	COBI
Cornus nuttallii	CONU4
Cornus sericea	COSE16
Cornus sessilis	COSE3
Cryptogamic crust	CRCR
Cupressus macnabiana	CUMA
Datura wrightii	DAWR2
Dendromecon rigida	DERI
Dichelostemma volubile	DIVO
Echinocactus polycephalus	ECPO2
Echinocereus engelmannii	ECEN
Elymus elymoides	ELEL5
Encelia farinosa	ENFA
Encelia virginensis	ENVI
Ephedra californica	EPCA2
Ephedra funerea	EPFU
Ephedra nevadensis	EPNE
Ephedra viridis	EPVI
Epilobium canum ssp. latifolium	EPCAL
Ericameria arborescens	ERAR27
Ericameria cooperi	ERCO23
Ericameria cuneata	ERCU7
Ericameria linearifolia	ERLA12
Ericameria palmeri var. pachylepis	ERPAP
Ericameria pinifolia	ERPI7
Eriodictyon crassifolium	ERCR2
Eriogonum cinereum	ERCI5
Eriogonum elongatum	EREL6
Eriogonum fasciculatum	ERFA2
Eriogonum heermannii var. heermannii	ERHEH2
Eriogonum inflatum	ERIN4
Eriogonum nudum	ERNU3
Eriogonum saxatile	ERSA6

Eriogonum wrightii	ERWR
Erioneuron pulchellum	ERPU8
Erodium cicutarium	ERCI6
Erysimum capitatum var. perenne	ERCAP
Eschscholzia californica	ESCA2
Escobaria vivipara	ESVI2
Ferocactus cylindraceus	FECY
Fraxinus dipetala	FRDI2
Fraxinus latifolia	FRLA
Fremontodendron californicum	FRCA6
Galium angustifolium	GAAN2
Garrya flavescens	GAFL2
Garrya fremontii	GAFR
Garrya veatchii	GAVE2
Grayia spinosa	GRSP
Gutierrezia microcephala	GUMI
Gutierrezia sarothrae	GUSA2
Hackelia mundula	HAMU
Hackelia velutina	HAVE
Hazardia squarrosa	HASQ2
Helianthemum scoparium	HESC2
Heteromeles arbutifolia	HEAR5
Holodiscus discolor	HODI
Hymenoclea salsola	HYSA
Hyptis emoryi	HYEM
Iris hartwegii	IRHA
Isomeris arborea	ISAR
Juglans californica	JUCA
Juncus balticus	JUBA
Juniperus californica	JUCA7
Juniperus occidentalis	JUOC
Juniperus osteosperma	JUOS
Krameria erecta	KRER
Krameria grayii	KRGR
Krascheninnikovia lanata	KRLA2
Larrea tridentata	LATR2
Lepechinia calycina	LECA3
Lepidium fremontii	LEFR2

Lepidospartum squamatum	LESQ
Leptodactylon californicum	LECA7
Lithocarpus densiflorus	LIDE3
Lithophragma bolanderi	LIBO5
Lonicera subspicata	LOSU2
Lonicera subspicata var. denudata	LOSUD
Lotus rigidus	LORI3
Lycium andersonii	LYAN
Lycium cooperi	LYCO2
Malacothamnus fasciculatus	MAFA
Malacothamnus fremontii	MAFR2
Malosma laurina	MALA6
Menodora spinescens	MESP2
Mimulus aurantiacus	MIAU
Mirabilis bigelovii	MIBI8
Muhlenbergia porteri	MUPO2
Nassella pulchra	NAPU4
Nicolletia occidentalis	NIOC
Nolina bigelovii	NOBI
Nolina parryi	NOPA
Opuntia basilaris	OPBA2
Opuntia echinocarpa	OPEC
Opuntia erinacea	OPER
Opuntia littoralis	OPLI3
Opuntia phaeacantha	OPPH
Opuntia ramosissima	OPRA
Petalonyx thurberi	PETH4
Peucephyllum schottii	PESC4
Phyllodoce breweri	PHBR4
Physalis crassifolia	PHCR4
Picea breweriana	PIBR
Pickeringia montana	PIMO5
Pinus albicaulis	PIAL
Pinus attenuata	PIAT
Pinus balfouriana	PIBA
Pinus balfouriana	PIBA
Pinus contorta	PICO
Pinus contorta murryana	PICOM

Pinus coulteri	PICO3
Pinus flexilis	PIFL2
Pinus jeffreyi	PIJE
Pinus lambertiana	PILA
Pinus monophylla	PIMO
Pinus monticola	PIMO3
Pinus muricata	PIMU
Pinus ponderosa	PIPO
Pinus sabiniana	PISA2
Pivea breweriana	PIBR
Platanus racemosa	PLRA
Pleuraphis rigida	PLRI3
Poa secunda	POSE
Populus balsamifera	POBA2
Populus fremontii	POFR2
Populus tremuloides	POTR5
Prosopis glandulosa	PRGL2
Prunus emarginata	PREM
Prunus fasciculata	PRFA
Prunus ilicifolia	PRIL
Prunus subcordata	PRSU2
Pseudotsuga macrocarpa	PSMA
Pseudotsuga menziesii	PSME
Psorothamnus arborescens	PSAR4
Psorothamnus emoryi	PSEM
Psorothamnus fremontii	PSFR
Psorothamnus spinosus	PSSP3
Pteridium aquilinum	PTAQ
Purshia tridentata	PUTR2
Quercus agrifolia	QUAG
Quercus berberidifolia	QUBE5
Quercus chrysolepus	QUCH2
Quercus cornelius-mulleri	QUCO7
Quercus douglasii	QUDO
Quercus durata	QUDU4
Quercus engelmannii	QUEN
Quercus garryana	QUGA4
Quercus john-tuckeri	QUJO3
Quercus kelloggii	QUKE

Quercus lobata	QULO
Quercus sadleriana	QUSA2
Quercus vacciniifolia	QUVA
Quercus wislizenii	QUWI2
Rhamnus californica	RHCA
Rhamnus crocea	RHCR
Rhamnus ilicifolia	RHIL
Rhamnus rubra	RHRU
Rhamnus tomentella	RHTO6
Rhus integrifolia	RHIXO
Rhus ovata	RHOV
Rhus trilobata	RHTR
Ribes californicum	RICA
Ribes indecorum	RIIN
Ribes malvaceum	RIMA
Ribes menziesii	RIME
Ribes roezlii	RIRO
Ribes speciosum	RISP
Rosa pinetorum	ROPI
Rubus discolor	RUDI2
Rubus ursinus	RUUR
Salazaria mexicana	SAME
Salix breweri	SABR2
Salsola tragus	SATR12
Salvia apiana	SAAP2
Salvia dorrii	SADO4
Salvia greatae	SAGR3
Salvia leucophylla	SALE3
Salvia mellifera	SAME3
Salvia mohavensis	SAMO3
Salvia sonomensis	SASO
Sambucus mexicana	SAME5
Sarracenia ×gilpinii Bell & Case [psittacina × rubra]	SAGI2
Schismus barbatus	SCBA
Senna armata	SEAR8
Sequoia sempervirens	SESE3
Sphaeralcea ambigua	SPAM2
Spiraea densiflora	SPDE

Sporobolus airoides	SPAI
Stanleya elata	STEL
Stephanomeria pauciflora	STPA4
Styrax officinalis var. redivivus	STOFR
Symphoricarpos rotundifolius	SYRO
Taeniatherum caput-medusae	TACA8
Taxus brevifolia Nutt.	TABR2
Thamnosma montana	THMO
Torreya californica	TOCA
Toxicodendron diversilobum	TODI
Trichostema lanatum	TRLA3
Tsuga heterophylla	TSHE
Tsuga mertensiana	TSME
Umbellularia californica	UMCA
Vaccinium ovatum	VAOV2
Vaccinium parvifolium	VAPA
Viguiera parishii	VIPA14
Viguiera reticulata	VIRE
Wyethia mollis	WYMO
Xylorhiza tortifolia	XYTO2
Yucca baccata	YUBA
Yucca brevifolia	YUBR
Yucca schidigera	YUSC2
Yucca whipplei	YUWH